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THE TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

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Clerk of Publications . . . G. B. STRATTON, M.B.E.

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DEGENERATIVE ARTERIAL DISEASE OF ANIMALS IN CAPTIVITY WITH SPECIAL REFERENCE TO THE COMPARATIVE PATHOLOGY OF ATHEROSCLEROSIS

BY

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AND

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The Zoological Society of London

[Accepted 9th February, 1960]

(With 4 plates)

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It is thought that extension of this preliminary survey to include a larger number of animals, together with a detailed study of their age, life history and diet, would be a valuable method of advancing knowledge of the pathogenesis of atherosclerosis.

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INTRODUCTION

The term arteriosclerosis, first introduced by Lobstein in 1833, means in its simplest form, hardening of an artery, and for many years was used to describe any type of degenerative arterial disease. Today, we recognize that arteriosclerosis probably expresses at least three distinct conditions, medial sclerosis (Mönckeberg's sclerosis), hypertensive arteriolosclerosis and atherosclerosis, and it is with the last that we are mainly concerned in this paper. Atherosclerosis is essentially a lesion of the arterial intima consisting of sclerotic changes associated with lipid deposits. In Man, there is little doubt of the

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prevalence of this condition during the last quarter-century, affecting particularly the coronary tree and associated with intravascular thrombosis. Almost every aspect of atherosclerosis has been extensively investigated, but apart from the exceptional work of Fox (1923, 1933 and 1939) and his successors at the Philadelphia Zoological Garden, there has been little systematic study of the comparative pathology of spontaneous arterial disease. Experimentally produced atherosclerosis, although of great value in emphasising the importance of any single causative factor, is of little use in gaining knowledge of atherosclerosis as it may occur in the wild or captive state in animals. We have had opportunity to examine material from the London Zoological Garden, from a number of different species, and have attempted to study arterial disease as it occurs today in these animals with particular reference to its relationship to human atherosclerosis.

MATERIAL AND METHODS

The heart and attached aorta were obtained from seventy-one animals that died in the London Zoo. Sixty of these specimens (twenty-five mammals, twenty-six birds and nine reptiles) were collected from consecutive post mortems during 1958 ; eleven further specimens of interest (two mammals and nine birds) collected at other times were also examined. The complete aorta was available for study in five cases only.

The distribution and macroscopic appearances of any lesions in the opened coronary arteries and aortæ were noted, and in order to facilitate recognition of small lipid deposits in the arterial walls the gross specimens were stained in many instances with Sudan IV. The technique used was similar to that employed by Holman *et al.*, (1958) on human material. In essence the method consists of immersing the aorta in a solution of Sudan IV and then removing the excess stain with ethanol. Bright red areas denoting the presence of stained lipid contrast with a diffuse pale pink staining of the other tissues.

Representative histological sections were prepared from the majority of the seventy-one specimens, and in several cases multiple blocks of tissue were examined. Frozen and paraffin-embedded sections were prepared and the stains used included : hæmatoxylin and eosin, Sudan IV and oil red 0 for fat, Verhoeff's elastic stain, Van Gieson's connective tissue stain, Gram and Ziehl-Neelsen stains for organisms, Rinehart and Abul Haj's modification of Hale's method for acid-mucopolysaccharides, Von Kóssa's method for calcium salts and Schultz's method for cholesterol.

RESULTS

Birds

Material from thirty-five birds was available for examination. Macroscopic lesions were seen in twelve aortæ and in a further four cases gross staining revealed a few tiny sudanophilic lipid foci in the intima of the vessel. The aortic lesions usually presented as raised, firm or hard, yellowish or whitish nodules and plaques on the intimal aspect of the vessel (Pl. 1, fig. 1); in other instances there was a more diffuse thickening and calcific rigidity of the vessel wall. The nodules were often strongly sudanophilic (Pl. 1, fig. 2). Gross

ulceration of the intimal surface with mural thrombus formation was not seen. In almost all our cases only a portion of the thoracic aorta and the attached roots of the brachio-cephalic vessels were received for examination, and it was not possible to comment on the distribution of these lesions throughout the arterial tree. The coronary vessels appeared normal in every case.

Histologically the lesions were of a common basic pattern, and were mainly confined to the intima. They consisted of areas of subendothelial intimal thickening composed of connective tissue in which were focal accumulations of lipid (Pl. 2, fig. 3).

The connective tissue varied from a loose areolar type to a more dense fibrosis, with pseudo-cartilaginous change (Pl. 2, fig. 4) in several specimens, and definite bone formation in two cases (P. 2, fig. 5). An excess of mucopolysaccharide material was often demonstrated.

The lipid was of two types, sudanophilic material and non-sudanophilic anisotropic crystals (Pl. 2, fig. 6 and Pl. 3, fig. 7). The sudanophilic form was found both extracellularly and intracellularly, and tended to be in the more superficial layer of the intima just deep to the endothelium, but some was also present in the deeper layer of the intima. The crystalline material was found principally in the deeper intimal layer, with a tendency for the long axes of the crystals to be arranged perpendicularly to the long axis of the vessel. This material was dissolved by fat solvents, and gave a positive reaction for cholesterol by the Schultz technique, and the crystals were converted to the characteristic "Maltese Cross" forms when gentle heat was applied to frozen sections.

Lesions, resembling those of human atherosclerosis in many respects, were seen in four parrots, a parrakeet, slender-billed cockatoo, peahen and peafowl, crested screamer, touraco, scarlet macaw, red-billed hornbill, Bahama duck, American widgeon and African cattle egret. The sub-endothelial osseous metaplasia was seen in one of the parrots and a cockatoo. There was considerable individual variation in the relative amounts of lipid and connective tissue present in the intimal lesions. For instance, the aortic plaques in a cattle egret were largely formed of fibro-chondroid elements and contained only a little lipid, whilst those from a touraco contained an abundance of both isotropic, sudanophilic droplets and anisotropic cholesterol crystals but showed little fibrosis and no calcification. In some sections from these fifteen birds, foci of mucoid degeneration, elastic fragmentation, fat deposition and early calcification were observed in the aortic media, but apart from the mucoid accumulation the medial changes were usually slight as compared with the intimal lesions.

A nodule of chondroid metaplasia with peripheral fibrosis, but not associated with lipid deposition, was found in the aorta from a goose and, in another goose, there was a small bacterial vegetation on the mitral valve of the heart.

No gross lesions were seen in the aorta or coronary arteries of the other eighteen birds examined. These included three ducks, a humming bird, curassow, Malayan bustard, ringed plover, sandpiper, herring gull, barn owl, parrakeet, cockatoo, black-footed penguin, emu, masked lovebird, red-billed pintail, spot-billed pelican and a Chinese goose.

Mammals

Specimens from twenty-seven mammals were available for examination. Eleven showed macroscopic changes in the aorta, and in five the lesions simulated human atherosclerosis. These specimens were obtained from two monkeys, two llamas and a giraffe. The lesions were generally small and few in number, and consisted of small raised nodules or yellowish streaks on the intimal aspect of the aorta (Pl. 3, fig. 8), except in the case of one llama where numerous raised calcified plaques were present. These areas measured up to 2×2 cm. in the thoracic segment with additional yellowish fatty streaking after staining with Sudan IV. The lipid was mainly in the form of sudanophilic droplets although cholesterol crystals were numerous in the aortic lesions of both llamas (Pl. 3, fig. 9), and, in one of these animals, chondroid and osseous metaplasia had developed in some of the harder nodules. In two further cases (a monkey and a chimpanzee) small sudanophilic intimal deposits were demonstrated by gross staining of the aorta with Sudan IV, the histological features of which were similar to the fatty streaking seen in human aortae (Pl. 3, fig. 10).

Small greyish intimal plaques and nodules were seen in aortæ from three wallabies. Histologically the lesions which bore no resemblance to human atheroma consisted of focal fragmentation and calcium encrustation of the elastic fibres at the junction of the intima and media (Pl. 4, fig. 11). Comparable, though less striking, microscopic lesions were present in a coronary artery from one of these wallabies, and an essentially similar change was observed in an aorta from a Soay sheep. Similar lesions have been found in the aorta and endocardium of horses, pigs and rabbits in a series apart from the London Zoo collection. In two of the three wallabies a few sudanophilic droplets were observed at the periphery of the aortic plaques.

The only other lesions observed were a large infective aneurysm of the ascending aorta in a vervet monkey and some eosinophilic material, probably of a sero-fibrinous nature, on and just beneath the intimal surface of the aorta from a rabbit, associated with a small thickened area seen macroscopically.

Aortæ from fourteen other mammals, including a monkey, chimpanzee, polar bear, tiger, kangaroo, galago, chinchilla, hare, dormouse, fishing cat, hamster, muntjac, sea-lion and civet appeared normal, although, as with the avian material, the complete aorta was not always available for examination. There was no macroscopic evidence of coronary arterial disease in any of the twenty-seven mammalian hearts but sections taken from the left atrium of the tiger's heart showed several small fibro-cellular thickenings of the endocardium.

Reptiles

The heart and aorta were examined from nine reptiles (three tortoises, three snakes, two crocodiles and an iguana). None showed any macroscopic lesions, and sections of the aortæ appeared normal macroscopically.

INCIDENCE OF LESIONS

The frequency of occurrence of aortic lesions in the sixty animals examined at consecutive post-mortems is shown in Table I. The number of specimens

TABLE I

Incidence of aortic lesions in sixty animals.

	Number examined	Number with atherosclerosis	Number with other aortic lesions
Mammals	25	5 (20 per cent)	5
Birds	26	8 (31 per cent)	—
Reptiles	9	—	—
TOTAL	60	13 (22 per cent)	

examined in this preliminary series is much too small to justify any detailed analysis of the incidence of atherosclerosis in the various orders and families of the mammals, birds and reptiles. It is hoped, however, that similar studies will be made on a considerably larger series of vertebrates, including amphibia and fishes.

DISCUSSION

Anatomically there is a fairly close similarity in structure of larger arteries in mammals, birds and Man. It might be expected, therefore, that the response to disease affecting these vessels would be similar in certain respects in all three species. Hitherto the term " arteriosclerosis " has been generally applied to arterial disease in mammals and birds where intimal thickening and fibrosis, lipid deposition, medial degeneration and calcification are present, although Fox (1933) recognized three distinct degenerative arterial lesions : hyperplastic intimal thickening, intimal atheroma (best illustrated in birds) and mid-mural calcification. The commonest arterial lesion in our material basically resembled the picture of atherosclerosis, and we consider that the term " atherosclerosis " should be substituted for " arteriosclerosis " in such cases to bring it into direct line with atherosclerosis in Man. We are not primarily concerned in this short paper with elastic degeneration of the sub-intima or with infective or parasitic arteritis or primary mucoid degeneration of the media.

From the slides and sections shown it would appear that atherosclerosis in mammals and birds bore a close resemblance to atherosclerosis in Man in three respects (Pl. 4, figs. 12, 13 and 14). Firstly, sub-endothelial intimal thickening and fibrosis were present ; secondly, sudanophilic material was present in the intima, and thirdly, doubly-refractile material, almost certainly cholesterol and cholesterol-esters, was found in the deeper intimal layer. This lipid was present in relatively small, early lesions in many of the specimens examined. Lindsay *et al.* (1952), and Lindsay & Chaikoff (1955) stated that lipid deposition was a relatively late occurrence in arteriosclerotic lesions in dogs and cats and that cholesterol was absent from the intimal plaques and thickenings. They commented that secondary lipid infiltration was more marked in birds than in cats and dogs. Microscopic aortic intimal fibrous lesions devoid of lipid have been reported in a gorilla by Steiner *et al.* (1955). More recently Lindsay & Chaikoff (1957) described arteriosclerotic lesions in two baboons; small amounts of lipid, including cholesterol, were found in fibrous intimal plaques secondary to degenerative changes in the internal elastic lamina and the localized deposition of

mucopolysaccharide substances. It is possible that diet and lipæmia have an important bearing on the production of these lesions and that this might account for the different picture in the specimens from the London Zoo.

Certain differences from atherosclerosis in Man were also apparent. In captive mammals and birds atherosclerosis rarely affected the coronary arterial tree. The aortic lesions did not proceed to local ulceration but tended to chondrify and even form bone. In no animal did we see any sizeable mural or occlusive thrombosis in the coronary vessels or aorta and it is interesting to speculate whether Man may have evolved a more complex system of blood clotting, relatively unstable in the presence of severe vascular disease. Medial degeneration may bear some relationship to overlying intimal disease and we would agree with Lloyd (1959) in his description of the frequent occurrence of mucoid degeneration of the media in Zoo animals. Further study on this aspect of arterial disase is in progress.

Fox has discussed the possible ætiological factors in the causation of arterial disease in animals but reached no firm conclusions. Examining a very large number of specimens, Fox, up to 1933, found an overall incidence of degenerative arterial disease in approximately 2 per cent of the material studied. In a later report, based on more recent material, Fox (1939) found arteriosclerosis in 13·7 per cent of birds examined and 15·4 per cent of mammals, although slightly less than 7 per cent of the birds and slightly less than 3 per cent of the mammals had atherosclerotic lesions. We have reviewed a very much smaller group and find atherosclerotic lesions in approximately 22 per cent of the animals examined.

Lack of detailed knowledge about arterial lesions in the wild state precludes any dogmatic statements concerning the problem of arterial disease in captive wild animals. From our limited material we have seen the most marked changes in the older parrots who were inactive birds but whose diet contained a very high proportion of essential unsaturated fatty acid. Whether or not any of these three factors, viz. age, amount of physical activity, or the quality of the diet bore any relationship to the production of arterial lesions is impossible to say from this preliminary survey. In one of the two llamas the gross lesions may have had some association with the varied diet that the twelve-year old animal enjoyed, having been born in the Garden and spent most of the time in the Childrens' Zoo. One thing is certain, longevity in animals at the London Zoo is increasing and a survey in some years time should show whether age is a significant factor in the production of atherosclerosis.

Since the commencement of this investigation, Ratcliffe & Cronin (1958) have reported that the incidence of arteriosclerosis in mammals and birds in the Philadelphia Zoological Garden has continued to rise, particularly since 1946 and they have suggested that social pressure, through an imbalance in adrenal secretion, has become a major factor in the frequency of arteriosclerosis. An earlier sudden increase in the incidence of arteriosclerosis in the quinquennium of 1931–1935 was tentatively correlated by these authors with a decrease in population and an increase in age of the animals on exhibition at that time. A high incidence of spontaneous aortic atherosclerotic lesions has been recorded very recently by Lofland & Clarkson (1959) in two breeds of pigeons (white

carneau and silver king), while two other breeds (racing homers and show racers) did not develop the disease. These differences could not be correlated with age, sex, diet or physical activity, and the authors suggested that atherogenesis in pigeons may result from an alteration of some metabolic factor that is genetically controlled.

Finally, we would suggest that the comparative pathology of arterial disease is an important method of study of the natural history of atherosclerosis. In the W.H.O. report of a study group on the Classification of Atherosclerotic Lesions (1958) the authors stressed the need to distinguish between the induced and naturally occurring arterial lesions. It is conceivable, however, that merely the detailed study of spontaneous arterial disease will provide further valuable knowledge of the pathology and pathogenesis of atherosclerosis.

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EXPLANATION OF PLATES

Plate 1

Fig. 1.—Ascending aorta of Scarlet macaw opened to show several raised, yellowish-white nodules on the intimal surface.

„ 2.—Base of heart and ascending aorta of Bahama duck, stained with Sudan IV, showing intimal plaques that are strongly sudanophilic.

Plate 2

Fig. 3.—Blue-winged parrot. Section of small aortic plaque, left upper field, showing thickened intima with sub-endothelial fat spaces. Haematoxylin and eosin. × 75.

„ 4.—Peafowl. Section of aortic plaque, showing pseudo-cartilaginous change in the thickened intima. H. and E. × 75.

„ 5.—"Old Bill", Slender-billed cockatoo. Section of aorta, showing bone formation in thickened intima. H. and E. × 75.

„ 6.—Crested screamer. Section of aorta, showing sudanophilic material in the superficial part of the intima and the crystalline structure of the deeper intimal layer. Media in lower half of field. Sudan IV. × 140.

Plate 3

Fig. 7.—Crested screamer. Crystalline material, as seen in Fig. 6 but photographed by polarised light, showing its anisotropic nature. × 120.

„ 8.—Llama. Aorta stained with Sudan IV, showing fatty streaking.

„ 9.—Llama. Aortic intima showing the crystalline structure of the deeper intimal layer. H. and E. × 280.

„ 10.—Woolly monkey. Section of small aortic nodule, showing focal intimal thickening with lipid deposition. Sudan IV. × 63.

Plate 4

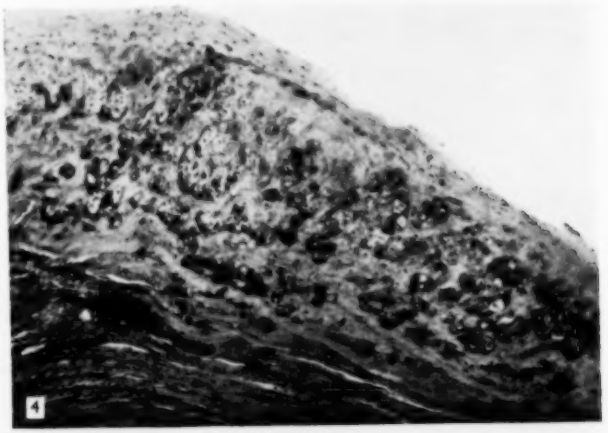
Fig. 11.—Wallaby. Section of aortic plaque, showing fragmented and calcified elastic fibres in the intima and inner media. H. and E. × 75.

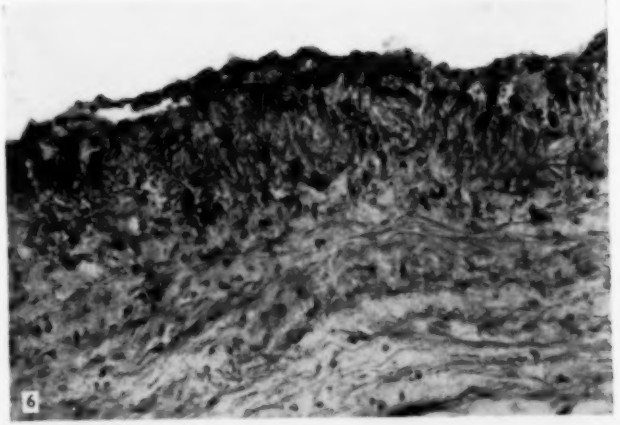
„ 12.—Human aorta. Section of early atherosclerotic lesion, showing intimal thickening and fat spaces. H. and E. × 20.

„ 13.—Human aorta. Section of atherosclerotic lesion, showing sudanophilic material in the more superficial part of the thickened intima, and some crystalline material in the deeper layer. Sudan IV. × 20.

„ 14.—Human aorta. Section of more advanced atherosclerotic plaque, with fibrous intimal thickening overlying cholesterol clefts. H. and E. × 20.

Degenerative arterial disease of animals in captivity.





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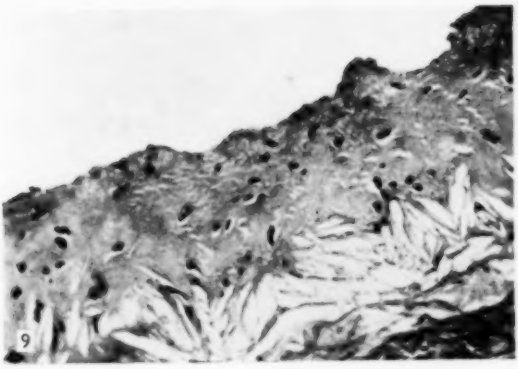

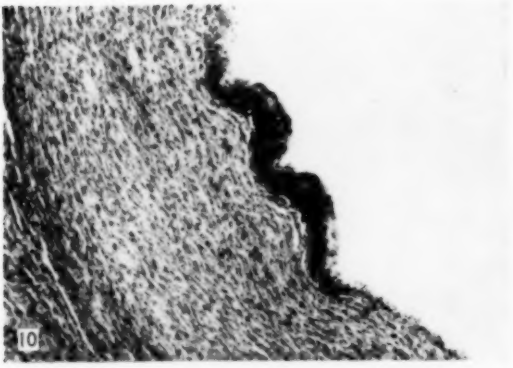

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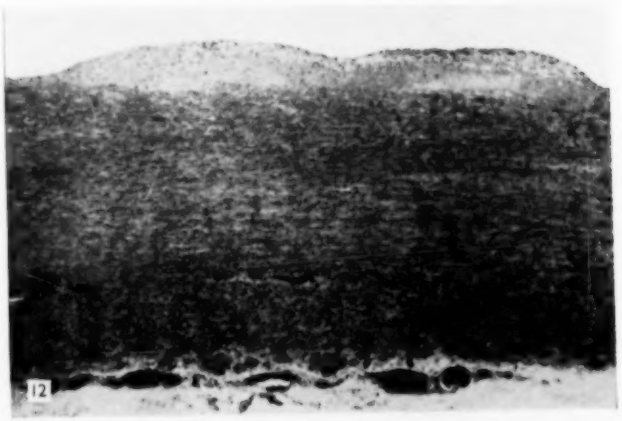

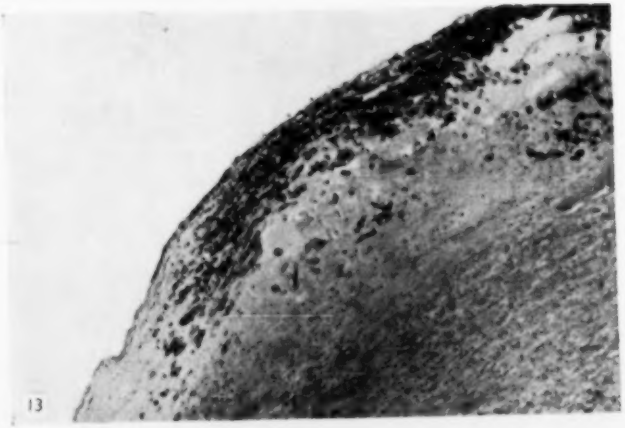

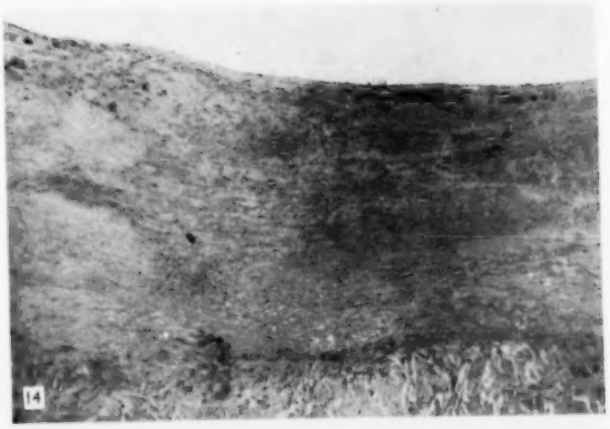

Degenerative arterial disease of animals in captivity.

REPORT ON A SMALL COLLECTION OF MYSIDACEA FROM SINGAPORE WATERS

BY

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(With 4 figures in the text)

A list of the species represented in the collection is given. Five of them are recorded for the first time since they were originally described and additional descriptive notes, with some figures, are given. Two species are recorded with some reserve and the differences shown by the present specimens from the published descriptions are fully discussed, with figures. One species, new to science, is fully described and figured.

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INTRODUCTION

Most of the hauls in which the present material was captured were taken at the Singapore Regional Fisheries Research Station's Permanent Station No. 5, which is situated about seven miles off shore in Singapore Strait (1° 14′N. 103° 55′E). One was taken immediately before sunset and the rest during the hours of darkness. Apart from two horizontal hauls taken just above the bottom, all the mysids taken at this Station were captured in vertical hauls from the bottom (82 m.) to the surface.

Four hauls were taken in the Prawn ponds off Malacca Strait and yielded very interesting results.

The present material does not by any means comprise an exhaustive collection of the Mysidacea in these waters, the specimens having been selected at random for identification by Mr J. Wickstead of H. M. Overseas Civil Service from some 650 plankton samples collected during the course of his work at the Singapore Regional Fisheries Research Station. They have, however, proved to be so interesting that a short preliminary account of them should be placed on record.

THE SPECIES REPRESENTED IN THE COLLECTION

Family **MYSIDA**

Subfamily **Siriellinae**

Genus *Siriella* Dana

Siriella vulgaris Hansen 1910

Siriella hanseni W. M. Tattersall 1922

Siriella singularis Nouvel 1957
Siriella ? inornata Hansen 1910

Subfamily **Rhopalophthalminae**

Genus *Rhopalophthalmus*

Rhopalophthalmus egregius Hansen 1910

Subfamily **Gastrosaccinae**

Genus *Gastrosaccus* Norman

Gastrosaccus indicus Hansen 1910
Gastrosaccus dunckeri Zimmer 1915
Gastrosaccus elegans sp. n.

Genus *Anchialina* Norman and Scott

Anchialina typica (Kröyer) 1861
Anchialina grossa Hansen 1910
Anchialina penicillata Zimmer 1915

Genus *Pseudanchialina* Hansen

Pseudanchialina pusilla (G. O. Sars) 1884

Subfamily **Mysinae**

Tribe Erythropini

Genus *Erythrops* G. O. Sars

Erythrops minuta Hansen 1910

Tribe Leptomysini

Genus *Promysis* Dana

Promysis orientalis Dana 1852.

Tribe Mysini

Genus *Nanomysis* W. M. Tattersall

Nanomysis insularis Nouvel 1957

Genus *Mesopodopsis* Czerniavsky

Mesopodopsis orientalis (W. M. Tattersall) 1908

Genus *Acanthomysis* Czerniavsky

Acanthomysis indica (W. M. Tattersall) 1922
Acanthomysis hodgarti (W. M. Tattersall) 1922

The type of *Gastrosaccus elegans* is lodged at the British Museum (Natural History) South Kensington, London.

Subfamily **Siriellinae**

Genus *SIRIELLA* Dana

SIRIELLA VULGARIS Hansen

Siriella vulgaris Hansen, 1910, p. 34, figs.; W. M. Tattersall, 1951, p. 62, figs.

Occurrence

Station 5. 15.7.55 (night). Vertical haul. 1 adult ♀ with empty brood sac, 6·5 mm.

1 small juv. ♀.

30.4.56. (night). Horizontal haul at bottom. 1 imm. ♂, 5 mm., 2 ♀♀ with well developed, empty brood sacs, 5 - 5·5 mm.

Distribution

Common in coastal waters of the Dutch East Indies (Hansen, 1910), Port Blair, Andaman Isles (Tattersall, 1922), Arabian Sea (Colosi, 1924), Peru and Hong Kong (Coifmann, 1937) ; Queensland and the Gt. Barrier Reef (Tattersall 1928, 1936), Philippines (W. M. Tattersall, 1951).

SIRIELLA HANSENI W. M. Tattersall

Siriella hanseni Tattersall, 1922, p. 448, figs.

Occurrence

Station 5. 15.7.55. (night) Vertical haul. 1 ♂, not quite mature, 6·5 mm., 1 badly damaged imm. ♂.

Remarks

These specimens differ from the published description and figures of the type in some of the proportions of the uropods and the telson. The exopod of the uropod is relatively rather more slender and its distal segment is longer. In the type the proximal segment is more than twice as long as the distal one, whereas in the present specimens it is only 1·7 times as long. The telson is also relatively longer than in the type and appears to be more slender. In all other respects the specimens agree so closely with the types that I have no hesitation in referring them to this species. Neither of the specimens is adult and it may be that the slight differences they display are due to their immaturity

Distribution

Known previously only from the Gulf of Manaar.

SIRIELLA SINGULARIS Nouvel

Siriella singularis Nouvel, 1957, p. 317, figs.

Occurrence

Tidal water from Prawn Pond at S.W. of Singapore Island.

7.9.54 (night). Outflowing. 3 adult ♂♂, 2 imm. ♂♂, 1 adult ♀, 7·5-8 mm. 4 juv.

7.12.54 (night). Inflowing. 16 adult ♂♂, 2 imm. ♂♂, 1 adult ♀ with empty brood sac 7-8 mm.

Remarks

The present specimens agree so closely in all details with the description and figures of this species given by Nouvel that I have no hesitation in referring them to it. They are somewhat smaller than Nouvel's adults (my largest specimen being only 7·5 mm. in length compared with 8·5 mm., the length of Nouvel's largest female) but it is possible that they may not be fully mature for none of the females was carrying eggs or embryos.

Distribution

Previously known only from brackish fish-breeding pools in eastern Java.

SIRIELLA INORNATA ? Hansen

Figs. 1 A - E

Siriella inornata Hansen, 1910, p. 36, figs.; W. M. Tattersall, 1928, p. 106; 1936, p. 146; 1951, p. 65.

Occurrence

Outflowing tidal water from Prawn Pond at night. 22.2.55 1 ♂ 8 mm. 1♀, with well developed empty brood pouch, 8 mm. 1 imm. ♀, 6 very small juv.

Remarks

I doubtfully refer these specimens to *S. inornata* for, whilst agreeing in general with the published description and figures of this species, they differ in the following characters :—

1. The rostrum is acutely pointed and extends forward to the level of, or beyond, the proximal third of the eyestalks.

2. In all specimens the antennal scale extends to the distal end of the antennular peduncle, or even slightly beyond it. Also the scale is relatively somewhat broader than in *inornata*. (Fig. 1 A)

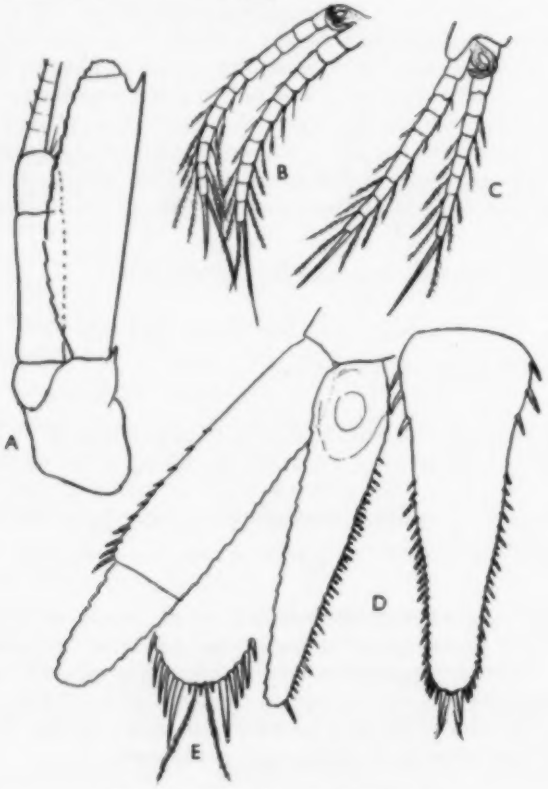

Fig. 1.—*Siriella inornata* ? Hansen

A. Right antenna of adult female × 38. B. Distal end of 3rd pleopod of the male × 38. C. Distal end of 4th pleopod of the male × 38. D. Telson and left uropod × 38. E. Apex of telson, enlarged.

3. *Size.* The largest specimens (which appear to be fully adult) measure only 8 mm. whereas Hansen records that adult males were 11-11·6 mm. and females 11·3 - 12 mm. in length.

The shape, proportions and relative length of the antennal scale, the form of the modification of the third and fourth pairs of pleopods of the male and the shape, armature and proportions of the uropods and telson (Figs 1 B-E) are so precisely like those figured for *S. chierchiae* Coifmann by W. M. Tattersall (as *S. occidentalis*) that the figures might have been made from the present specimens. Were it not for the fact that *S. chierchiae* is a very common form in the tropical western Atlantic and is not known from any other locality, I should be inclined to refer these specimens to that species.

Distribution

Dutch East Indies, Philippines and off the coast of Queensland. The species is recorded as being abundant close in shore at the surface at night.

Sub-family **Rhopalophthalminae**

Genus *RHOPALOPHTHALMUS* Illig

RHOPALOPHTHALMUS EGREGIUS Hansen

Rhopalophthalmus egregius Hansen 1910, p. 49, figs.; O. S. Tattersall 1957, p. 87, figs.

Occurrence

Tidal water from Prawn Pond.

7.9.54. (night), outflowing 1 adult ♂ ,10 mm. 3 juv.

7.12.54 (night), inflowing, 1 adult ♂, 2 adult ♀♀ (1 ovig.), 4 juv.

Remarks

Since the types of this species were captured by the " Siboga " Expedition, many records of it have been made from very widely separated areas. After a complete re-examination of all the known material which had been referred to the species and a further examination of the type material, O. S. Tattersall (1957) found that no fewer than five distinct species were contained therein. None of these was the true *R. egregius* Hansen. It is therefore most gratifying and satisfactory to find in the present collection several specimens in beautiful condition which can unquestionably be referred to *R. egregius.*

Distribution

Hitherto known only from Sangkapoera-roads, Bawean Is. in 12 m., collected by the " Siboga " Expedition.

Sub-family **Gastrosaccinae**

Genus *GASTROSACCUS* Norman

GASTROSACCUS INDICUS Hansen

Gastrosaccus indicus Hansen, 1910, p. 56, figs.

Occurrence

Station 5. 15.7.55 (night), vertical haul from bottom (82 m.) International coarse silk net, 58 m.p.i. 1 imm. ♂, 1 very small juv. ♂, 1 juv. ♀.

17.5.56 (night), vertical haul, 1 juv. ♀.

Distribution

Dutch East Indies (Hansen 1910; Java (Delsman 1939); N.E. of Madagascar (W. M. Tattersall 1911) ; Philippines (W. M. Tattersall 1951).

GASTROSACCUS DUNCKERI Zimmer

Figs. 2 A - N

Gastrosaccus dunckeri Zimmer, 1915, p. 165, figs.; Tattersall, 1922, p. 459. O.S. Tattersall, 1958, p. 375.

Occurrence

Station 5. 23.9.55 (night), horizontal bottom haul, 1 adult ♂, 4 ovig. ♀♀, 9 - 9·5 mm.

17.5.56 (night), vertical haul from bottom (82 m.) to surface, stramin net, 11 adult ♂♂, largest 9 mm., 2 adult ♀♀, 7·5 - 8 mm., 1 juv. ; international coarse silk net, 58 m.p.i. 1 adult ♂, 9 mm., 1 nearly adult ♀, 2 juv.

Remarks

The present specimens closely resemble the published description and figures of *Gastrosaccus dunckeri* in so many of their characters that, although they do exhibit some decided variations, I feel, albeit with some little reserve, that they should be referred to this species.

All the specimens agree with Zimmer's description of the type in size, general form, relative size of the carapace, the relative lengths of the antennules and antennae and eyes, the form and armature of the antennular peduncle, the relative proportions of the tail fan, the armature of the uropods and the shape of the telson. They do, however, present some marked differences as follows :—

1. *Carapace.* According to Zimmer (p. 165) the anterior margin of the carapace is " vorn scharfwinkelige Stirnplatte ausgezogen " and in his figure he shows an acutely pointed rostral plate extending almost to the level of the proximal margin of the cornea. In all the present specimens the rostrum is as figured in Figs. 2 A - B, that is, with the anterior end bluntly rounded and extending only to the level of the middle of the eyestalk. The lateral margins of the rostrum and around the blunt apex are sharply uptilted (Fig. 2 B) so that the rostrum is trowel-shaped and its margins are extremely difficult to make out. There is a pseudorostral projection, however, which can be clearly seen lying below and anterior to the true rostrum and this is of the same shape and occupies precisely the same position as indicated by Zimmer for his rostrum. It is possible that he mistook this for the true rostrum.

It is, however, in the form of the posterior margin of the carapace that the greatest difference between the present material and Zimmer's type of *G. dunckeri* is found. He mentions particularly that there are two reflexed lappets present, similar to those found in *G. sanctus* but considerably longer. Among the present material I have found every gradation from only the merest trace of lappets as seen in Fig. 2 A to quite long, sharply pointed, forwardly directed lappets as in Fig. 2 C. These differences are not correlated with size or sex. I have found diversity of the same kind in the size of the lappets occurring in *G. sanctus*, in specimens which conformed with the greatest exacti-

tude to the descriptions of that species in all their other characters. It would appear therefore that this character does not constitute a reliable guide for the identification of species of the genus.

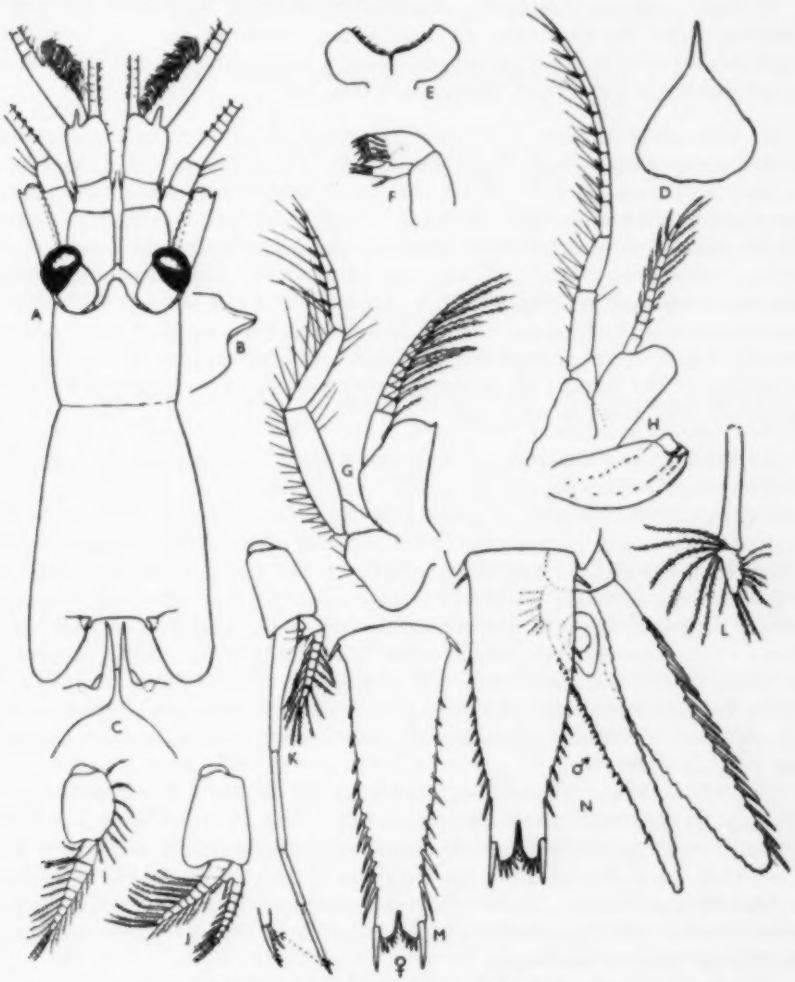

Fig. 2.—*Gastrosaccus dunckeri* Zimmer.

A. Anterior end of adult male in dorsal view. × 16. B. Anterior end of carapace in dorso-lateral view. C. Posterior end of carapace of specimen captured 23.9.55. D. Labrum × 44. E. Labium × 44. F. Maxillule × 44. G. Third thoracic appendage × 32. H. Eighth thoracic appendage × 32. I. First pleopod of male × 24. J. Second pleopod of male × 24. K. Third pleopod of male × 24. L. First pleopod of female × 24. M. Telson of adult female × 36. F. Telson and right uropod of adult male × 36.

2. *Antennal scale.* The scale is relatively a little broader in the Singapore specimens than in Zimmer's type, being less than three times as long as broad compared with three and one third in his ; the tooth terminating the outer

margin is as long as, or even longer than the apex of the scale whereas in Zimmer's figure it is distinctly shorter. (Fig. 2 A).

3. *Eyes.* Zimmer definitely states that the eyes are small with the cornea narrower than the eyestalk. In the present material they are relatively larger, wholly uncovered by the anterior margin of the carapace and the rounded cornea definitely wider than the eyestalk (Fig. 2 A).

4. *Pleopods of the male.* The only important difference to be found in these appendages is in the form of the distal end of the exopod of the third pair. Zimmer says that there is a small distal segment in addition to the normal four segments found in the "*normani*" type in the genus, and adds that it bears a small strong barbed seta, while the penultimate segment bears a single strong "befiederter Dorn". I am unable to find this formation in any of the numerous males at my disposal (Figs. 2 I-K). The *first pleopod of the female* is not mentioned by Zimmer. In the present female specimen I am unable to see any trace of an exopod and the first pleopods appear to be definitely uniramous. The distal end of the sympod is armed with about half a dozen extremely long plumose setae (Fig. 2 L).

5. *Telson.* The telson in all the present specimens is relatively somewhat broader than in Zimmer's figure. The number and disposition of the spines arming the lateral margins is almost precisely as he figures and describes with the considerable gap between the distal lateral spine on each side and the large apical spine. This gap and the widening of the telson posterior to the last lateral spine is strikingly alike in Zimmer's specimens and these from Singapore Strait. There is, however, a marked difference in the size of the lateral spines. These in the present material are considerably larger than in Zimmer's type especially towards the posterior end of the row. In addition there is quite marked sexual dimorphism in this respect. In all females, irrespective of their age and size, the lateral spines are much longer than in males of comparable size (Figs. 2 M-N).

In both sexes the telson is hollowed from above; as a result the marginal spines point somewhat obliquely upward from the uptilted lateral margins and, in dorsal view, appear to be much shorter than they actually are. It is only when they are flattened down by the pressure of a cover-slip that their true size can be clearly seen. Zimmer does not comment upon any sexual differences in the telson. His figure is of a male and even in this the spines are shorter than in the present specimens.

The cleft of the telson varies somewhat in depth but in all the Singapore specimens it is deeper and narrower than as figured by Zimmer for the type.

I have examined specimens from the Puri Beach, Orissa which were referred to *G. dunckeri* by the late W. M. Tattersall (1922). In all of these the lappets from the posterior margin of the carapace are remarkably well developed, but the anterior margin of the carapace, the proportions of the antennal scale, the form of the distal end of the third pleopod of the male and the size of the spines arming the lateral margins of the telson are in complete agreement with the Singapore material.

Distribution

Captured during a voyage between Ceylon and New Guinea (Zimmer, 1915); Puri Beach, Orissa, India (Tattersall, 1922); off Trivandrum, India (Pillai, 1957); off Portuguese East Africa (O. S. Tattersall, 1959).

GASTROSACCUS ELEGANS sp. n.

Figs. 3 A-I.

Occurrence

Singapore Regional Fisheries Research Station 5, vertical hauls from bottom (82 m.) to surface, in darkness.

15.7.55. I.C.S.N., 58 m.p.i., 3 juv. ♂♂, 5-6 mm., 1 adult ♀, 6·75 mm., 1 juv. ♀.

16.7.55. Stramin net, 1 ovig. ♀, 8 mm., TYPE, 1 adult ♀ with empty brood sac, 8 mm.

17.5.56. 1 adult ♂, 7·5 mm., 3 imm. ♂♂, 1 adult ♀ with empty brood sac, 1 imm. ♀.

Description

General form slender, delicate and graceful. *Carapace* produced anteriorly into a short, bluntly rounded rostrum with its lateral margins diverging at about 45°; extending forward as far as the outer margin of the cornea of the eyes; no marked "shoulders". Posterior margin with somewhat shallow, widely open emargination, bearing on each side a short, inwardly directed, bluntly rounded lappet (Figs. 3 A-B).

Antennules relatively long and robust in both sexes; outer margin of second segment armed with three slender spines; inner margin of third segment armed with six long, strong, plumose setae; basal segment of outer flagellum swollen and armed in both sexes with sensory setae (Figs. 3 A, C).

Antennae. Scale slender, four times as long as broad, extending forward to the level of the distal margin of the second segment of the antennular peduncle; apex narrow and only slightly longer than the tooth which terminates the outer margin; small distal articulation present. *Peduncle* extending to the middle of the third segment of the antennular peduncle; inner margins of the second and third segments armed with a few long plumose setae (Figs. 3 A, D).

Eyes small, with the cornea narrower than the eyestalks and set obliquely, facing outward (Fig. 3 A).

Labrum produced forward in the median line into a very long, slender spine-like process which is flanked on each side with four or five short graduated spines (Fig. 3 E). A similar form of ornamentation of the anterior margin of the labrum is found in *Gastrosaccus kojimaensis* (Nakazawa 1910, p. 254).

Thoracic appendages slender, with the carpopropodus of the third and fourth pairs composed of 6-7 subsegments, fifth of 8, sixth of 9, seventh of 10 and eighth of 12 (Figs. 3 F-G).

Pleopods of the male. First, fourth and fifth pairs with normal exopods, composed of 8, 9 and 10 segments respectively, and small unsegmented endopods; second pair biramous with segmented rami of equal length, each composed of 9 segments; exopod considerably more robust than the endopod but not otherwise modified; third pair with normal segmented endopod; exopod elongate, extending to the proximal margin of the telson, composed of four

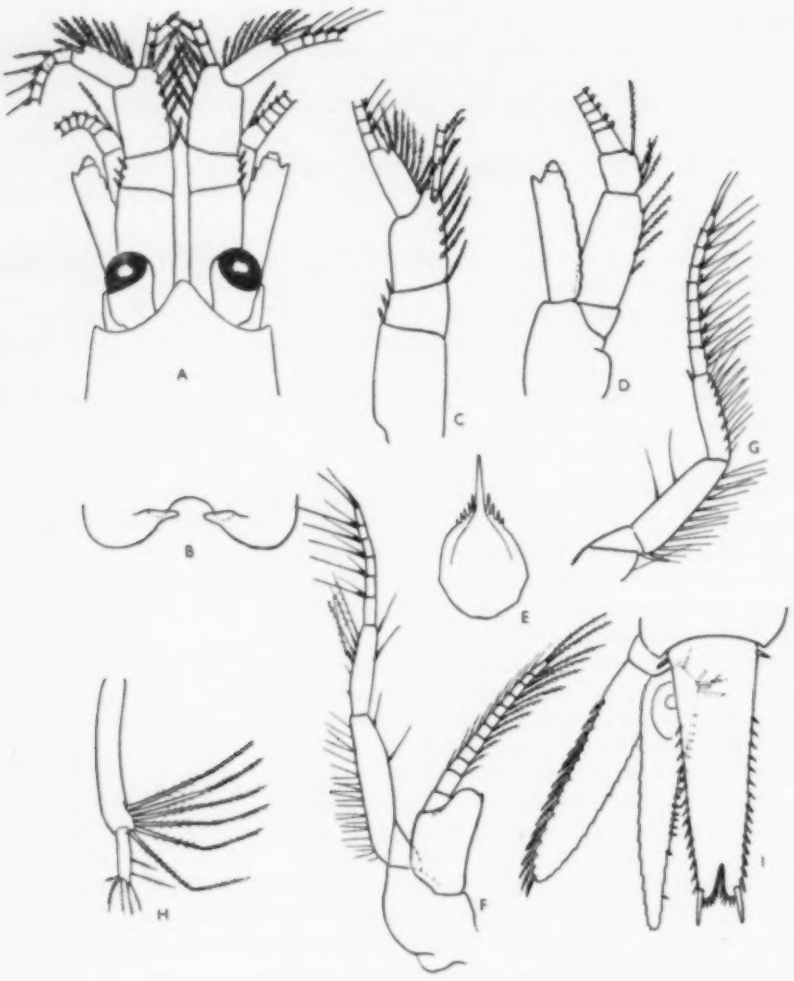

Fig. 3.—*Gastrosaccus elegans* sp. n.
A. Anterior end of adult female in dorsal view × 36. B. Posterior margin of carapace in dorsal view × 36. C. Antennule × 36. D. Antenna × 36. E. Labrum in ventral view × 44. F. Third thoracic appendage × 36. G. Endopod of eighth thoracic appendage × 36. H. First pleopod of female × 44. I. Telson and left uropod in dorsal view × 36.

segments and terminating in two small barbed setae. *First pleopod of the female* unusually long, uniramous, distal end of the sympod armed with exceptionally long plumose setae (Fig. 3 H).

Uropods. Endopods slightly longer than the exopods and extending to the distal ends of the long apical spines of the telson ; outer margin of exopod armed with 16-17 long slender spines ; inner margin of endoped armed with

a close row of short blunt spines extending evenly from the region of the statocyst for two thirds of the length of the margin, distal third of the margin armed with two widely spaced spines as in Fig. 3 I.

Telson long and slender, almost three times as long as broad at the base ; lateral margins straight, each armed with one large basal spine and a regular row of 15-16 small, almost equal spines extending evenly along the distal two thirds of the margin ; apical spines three times as long as the lateral ones. *Cleft* narrow, one eighth of the length of the telson in depth (Fig. 3 I).

Length largest male, 7·5 mm., ovigerous females 7 - 7·5 mm.

Remarks

This species can be recognized by its slender graceful form, by the relatively small eyes with the cornea set obliquely on the eyestalk, by the small inwardly-directed lappets on the posterior margin of the carapace, the armature of the endopod of the uropod, the long telson with its straight lateral margins and the very regular spines which extend right to the apical spines. One very marked character of this species is the peculiar form of the labrum with its unusually long anterior projection and the small graduated spines which flank it. The whole labrum is large and conspicuous and can readily be seen from the ventral side of the animal without dissection. Nakazawa (1910) has described a similar form of labrum in *G. kojimaensis* but *G. elegans* can be distinguished from this Japanese species by the presence of lappets on the posterior margin of the carapace ; by the fewer, smaller spines arming the inner margin of the endopod of the uropod and, above all, by the small spines arming the lateral margin of the telson. Nakazawa did not figure the telson of his type but he specifically stated concerning the telson that the lateral margin was " armed with 14 spines, the last of these being remarkably long ".

Type. Brit. Mus. (Nat. Hist.) 1960. 3. 28. 1-6.

Genus *ANCHIALINA* Norman and Scott

Anchialus Kröyer 1861.
Anchialina Norman & Scott, 1906.

ANCHIALINA TYPICA (Kröyer)

Anchialus typicus Kröyer 1861, p. 53, figs.
Anchialina typica Hansen 1910, p. 52, 1912, p. 196.
Anchialina typica W. M. Tattersall, 1951, p. 100.
Anchialina typica O. S. Tattersall, 1955, p. 89.

Occurrence

Station 5. 20.4.56 (night). Bottom horizontal haul. 1 nearly adult ♂, 4·5 mm., 1 smaller ♂, posterior end of large ♀., 1 juv. ♀.

Station 5. 17.5.56 (just before sunset), Vertical haul from bottom (82 m.) to surface, Stramin net. 1 adult ♀, 4.5 mm.

Distribution

Widely distributed in the warmer coastal waters of the western Pacific, China Seas and Gt. Barrier Reef ; Hawaii, Philippines, East Indies ; Andaman

Isles, Gulf of Manaar ; West Indies, Bermuda, tropical waters of western Atlantic from the southern United States to mid-Atlantic ; west of Orange River Estuary in the East Southern Atlantic.

ANCHIALINA GROSSA Hansen

Anchialina grossa Hansen, 1910, p. 54, figs.; 1912, p. 96.
Anchialina grossa, W. M. Tattersall, 1922, p. 458, figs.; 1936, p. 148 ; 1951, p. 102.
Anchialina frontalis Zimmer, 1915, p. 159, figs.

Occurrence

Station 5. 16.7.55 (night) Vertical haul from bottom (82 m.) to surface. 2 small juv. ♀♀.

Station 5. 17.5.56 (night). Vertical haul from bottom to surface. 1 adult ♂, 1 juv. ♀, 1 smaller juv.

Distribution

Bay of Bengal, Gulf of Siam, Dutch East Indies (Hansen, 1910) ; Gilbert Islands (Hansen, 1912) ; Bay of Bengal (Zimmer, 1915) ; India (W. M. Tattersall, 1922) ; Gt. Barrier Reef (W. M. Tattersall, 1936) ; Philippines (W. M. Tattersall, 1951).

ANCHIALINA PENICILLATA Zimmer

Anchialina penicillata Zimmer, 1915, p. 161, figs.
Anchialina penicillata W. M. Tattersall, 1940, p. 331 ; 1951, p. 103.

Occurrence

Station 5. 16.7.55. (night). Vertical haul from bottom (82 m.) to surface. 1 adult ♂, 7·5 mm., 1 imm. ♀.

Distribution

The type specimen was captured during a voyage from Ceylon to Dampier Strait (Zimmer, 1915) ; New South Wales (W. M. Tattersall, 1940) ; Marshall Islands, Philippines (W. M. Tattersall 1951). The species is rare and has never been taken in large numbers. The greatest number to be captured at a time was six off New South Wales. A few more were recorded from the Philippines but in this case some hauls were put together.

Genus *PSEUDANCHIALINA* Hansen

PSEUDANCHIALINA PUSILLA (G. O. Sars)

Figs. 4 A-C.

Promysis pusilla G. O. Sars, 1883, p. 42.
Anchialus pusillus, G. O. Sars, 1885, p. 200, figs.
Pseudanchialina pusilla Hansen, 1910 p. 60, figs.; W. M. Tattersall 1936, p. 149 ; Pillai, 1957, p. 9, figs.

Occurrence

Malacca Strait, N. of Sumatra (7° 13′ N., 97° 12′ E). Surface townet at night over 350 fms. with International Coarse Silk Net, mesh 58 m.p.i. 2 adult ♂♂, 3 mm., badly damaged.

Malacca Strait, entrance to western Java Sea. 2 adult ♂♂, 2·8 - 3·0 mm., 1 adult ♀, with empty brood sac, 3 mm., 3 small juv.

Remarks

The specimens are not in good condition and it is very difficult to make out the true shape of the anterior end of the carapace. In none of them could I see the broad, obtusely rounded rostral plate as figured by Hansen. One female is less damaged than the others and in this specimen the rostrum appears as in Fig. 4 A. This specimen differs from the others in having a small supplementary tooth on the outer margin of the antennal scale immediately proximal to the normal terminal tooth (Fig. 4 A).

The telson, which is in good condition in all the present specimens, is somewhat broader than that figured by Hansen and its lateral margins are less concave. The armature of the margins and of the cleft, the shape and depth

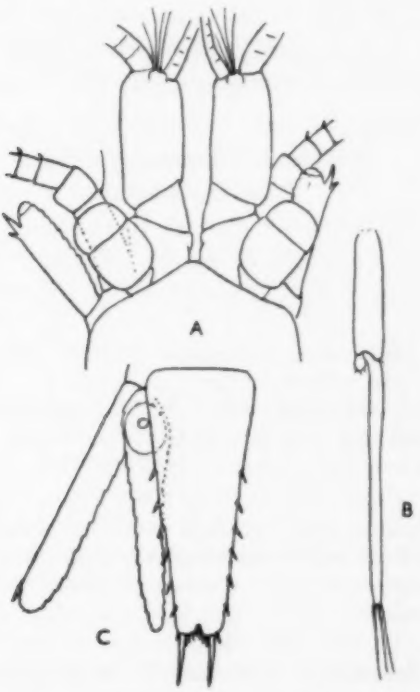

Fig. 4.—*Pseudanchialina pusilla* (G. O. Sars).
A. Anterior end of adult male × 60. B. Third pleopod of male × 60. C. Telson and left uropod of adult male × 60.

of the cleft and the form and proportions of the uropods conform closely to those figured by Hansen (Fig. 4 C). Hansen described, but did not figure, the fourth pleopod of the male and I am pleased to be able to give a figure of it here (Fig. 4 B).

I am not able to make out any lateral lamellae from the first abdominal somite in the female. The adult female in this collection has a large, clear

marsupium but I can see no trace of lamellae and must conclude that they are not present.

Pillai (1957) described and gave small but very clear figures of an ovigerous female from the coast of Travancore. He referred it to *P. pusilla* but, from a close study of his figures and from his brief description, I suspect that he may be dealing with a new species of the genus. The form of the antennal scale with the tooth terminating the outer margin shorter than the apex and the absence of a distal suture, the " small anterior point " of the rostrum, the very shallow cleft of the telson and its long lateral spines appear to be sufficiently distinctive to warrant the formation of a new species. It is to be hoped that further specimens may become available for further study, and that male specimens can be examined.

Distribution

Celebes Sea (G. O. Sars, 1885) ; East Indies and Bay of Bengal (Hansen, 1910) ; Gt. Barrier Reef (Tattersall, 1936) ; off Trivandrum, Travancore (Pillai, 1957).

Sub-family **Mysinae** Hansen

Tribe Erythropini

Genus *ERYTHROPS* G. O. Sars

ERYTHROPS MINUTA Hansen

Erythrops minuta Hansen, 1910, p. 63, figs.; W. M. Tattersall, 1922, p. 462, figs.

Occurrence

Station 5. All hauls taken in darkness. 15.7.55. Net N 70, Vertical haul from bottom (82 m.) to surface. 1 juv. ♀.

20.4.56. Horizontal bottom haul. 1 adult ♂, 2.8 mm., 1 imm. ♀, 2·5 mm.

17.5.56. Vertical haul from bottom to surface 4 juv. ♀♀. 2 mm.

23.9.55. Horizontal bottom haul. 1 ovig. ♀.

Remarks

The present specimens agree faithfully with the description given by Hansen for the species and I am able to confirm the sexual dimorphism in the relative lengths of the spines arming the posterior margin of the telson which was recorded by him.

Distribution

Gulf of Siam (Hansen) ; G. of Manaar (W. M. Tattersall, 1922).

Tribe Leptomysini

Genus *PROMYSIS* Dana 1850

Promysis Dana, 1850, p. 130.
Uromysis Hansen, 1910, p. 71.

PROMYSIS ORIENTALIS Dana

Promysis orientalis Dana, 1852, p. 651 ; 1855, pl. 43, figs. 4 a-c.; W. M. Tattersall, 1936, p. 154, fig. 5.; 1951, p. 151.
Uromysis armata Hansen, 1910, p. 72, figs.; Colosi, 1918, p. 9 : 1920, p. 24.
Promysis armata W. M. Tattersall, 1923, p. 285.

Occurrence

5° 34′ N., 97° 49′ E (northern entrance to Malacca Strait). 26.2.56 (night), vertical haul from bottom (92 m.) to surface. 1 adult ♀ with empty brood pouch, 2 juv.

Remarks

The specimens agree remarkably closely with the published descriptions and figures of the species especially in respect of the peculiar armature of the endopod of the uropod and in the form of the telson.

Distribution

China Seas (Dana 1852 ; Colosi 1918, 1920) ; between Ceylon and New Guinea (Zimmer, 1915) ; Sulu Archipelago (Hansen, 1910) ; Philippines (Tattersall, 1951) ; Great Barrier Reef (Tattersall, 1936). The species appears to be planktonic in upper waters, especially at night.

Tribe Mysini

Genus *NANOMYSIS* W. M. Tattersall

NANOMYSIS INSULARIS Nouvel

Nanomysis insularis Nouvel, 1957, 0. 323, figs.

Occurrence

Tidal waters from Prawn Pond, Singapore Island (night hauls).

7.9.54. Outflowing. 8 adult ♂♂, 1 juv ♂, 1 ovig. ♀ 3 juv. ♀♀, 4 - 4·5 mm.

7.12.54. Inflowing. 2 adult ♂♂, 1 adult ♀, (empty), 1 juv. ♀, 3 very small juv.

Remarks

I have re-examined specimens of *Nanomysis siamensis* W. M. Tattersall in the collections of the late W. M. Tattersall and am able to confirm that *siamensis* and *insularis* differ as follows :—

1. *Rostral plate* short and acutely pointed in *siamensis*, evenly arcuate in *insularis*.

2. *Uropods*. Exopod only very slightly longer than endopod in *siamensis* but half as long again in *insularis*.

3. *Fourth pleopod of the male* extending to the distal end of the telson in *siamensis* but barely reaching beyond the proximal margin in *insularis*.

Tattersall's material is in bad condition and contains only one male so that it has not been possible to ascertain whether there are any sternal processes on the thoracic somites in males of *siamensis*. In the present material these processes are very well developed and appear to be longer than as shown by Nouvel though they agree exactly with his figures in their general form.

In one adult male the thoracic endopods and the antennules were infested with a large number of an epizoic protozoan each borne on a long, extremely delicate stalk.

Distribution

Previously known only from the fish-rearing ponds near Surabaja in Eastern Java.

MESOPODOPSIS ORIENTALIS (Tattersall)

Macropsis orientalis Tattersall, 1908, p. 236, figs.
Mesopodopsis orientalis Tattersall, 1922, p. 482 ; Nair, 1939, p. 175.

Occurrence

Outflowing tidal water from Prawn Pond, S.W. area of Singapore Island. Three night hauls taken in October, 1955.

1. 24 adult ♂♂, 26 ♀♀, only a few ovigerous, 5 - 5·5 mm.
2. More than 250—breeding, with few juveniles.
3. Several hundreds—many breeding.

Distribution

Coasts of the Bay of Bengal from the Ganges Delta to Madras ; coasts of Cochin and Goa (Tattersall) ; fish-rearing lagoons of Java (Nouvel).

Genus *ACANTHOMYSIS* Czerniavsky

ACANTHOMYSIS INDICA (W. M. Tattersall)

Neomysis indica W. M. Tattersall, 1922, p. 483, figs.; Pillai, 1957, p. 14.

Occurrence

Station 5. All night hauls.

23.9.55. Horizontal bottom haul, 1 adult ovigerous ♀, 6·5 mm., 1 adult ♀, 6·4 mm.

20.4.56. Horizontal bottom haul, 2 juv. 3 mm.

17.5.56. Stramin net. Vertical haul from bottom (82 m.) to surface, over 60, nearly all breeding, average size 5·5 - 6 mm.

17.5.56. Net N 50. Vertical haul from bottom to surface, 2 adult ♂♂, 6 mm. 6 ♀♀, 5·0 - 5·5 mm., 3 juv.

Distribution

Port Blair, Andaman Islands ; Gulf of Manaar ; Mormugoa Bay, Portuguese India (Tattersall, 1922) ; off Trivandrum, Travancore (Pillai, 1957). The present records extend the known distribution of the species considerably to the eastward.

ACANTHOMYSIS HODGARTI (W. M. Tattersall)

Neomysis hodgarti W. M. Tattersall, 1922, p. 286, figs.

Occurrence

Station 5. All hauls taken in darkness.

15.7.55. Vertical haul from bottom (82 m.) to surface. A few very small juv., posterior end of adult ♀.

20.4.56. Horizontal bottom haul. 1 adult ♀, 5·5 mm.

17.5.56. Vertical haul from bottom to surface. Stramin net. 1 adult ♂, 7 mm., 1 juv., ♂. 1 adult ♀ 6 mm., 1 ♀ 5·5 mm., 1 juv. ♀.; net N 50. 1 adult ♂ (badly damaged, 1 ovig.) ♀, 6 mm.

Distribution

Hitherto known only from the mouth of the Sarawak River, Borneo.

ACKNOWLEDGMENTS

I am greatly indebted to Mr J. Wickstead of H. M. Overseas Civil Service for allowing me to examine this material and for supplying me with hydrographical information of the habitat in which the animals were living, and I wish to express my gratitude to Dr I. Gordon for reading the manuscript.

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OBSERVATIONS ON THE BANDED ANT-EATER *MYRMECOBIUS F. FASCIATUS* WATERHOUSE (MARSUPIALIA), WITH PARTICULAR REFERENCE TO ITS FOOD HABITS

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(With 1 plate and 1 figure in the text)

New observations are recorded on the banded ant-eater or numbat (*Myrmecobius f. fasciatus* Waterhouse), of south-western Australia. It lives in shrub woodland in which the majority of trees are eucalypts (chiefly *E. redunca* Schau. var. *elata* Benth.), the heartwood of most of which are eaten out by the termite, *Coptotermes acinaciformis* (Frogg.). The woodland floor is strewn with fallen hollow limbs and logs with which the animal is associated and runs to when disturbed.

The past and present geographical distribution has been examined, showing a considerable shrinkage of range since European occupation. The subspecies *M. f. rufus* Wood Jones is recorded in Western Australia for the first time.

The nominate race is diurnal and in general is solitary, and observations suggest that it holds some sort of territory. Its general daily behaviour and feeding methods are described. The food habits were determined chiefly from scat analysis. It lives largely on termites scratched from the soil, but ants make up about 15 per cent of its diet. All species of termites are eaten, roughly in proportion to their abundance and availability, but the bulk of ants eaten are the small predatory species. The numbat probably does not search for ants but these are ingested incidentally when they swarm in to prey on the exposed termites.

The young, of which there are normally four, are born from summer to autumn or early winter (January to April or May) and are carried or nursed by the mother through the winter. There is evidence of a seasonal cycle of fertility in the male.

Observations are also given on growth of young, voice, adult weight, parasites, possible predators, and other subjects.

The reasons for the numbat's decline are discussed and some suggestions are given regarding its conservation.

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INTRODUCTION

The banded ant-eater (*Myrmecobius f. fasciatus* Waterhouse) or numbat, as it is commonly called after one of its aboriginal names, is an aberrant dasyurid highly specialized as a termite- and ant-feeder. Because of its bright coloration and interesting habits, it is probably the most attractive of all the marsupials. Pl. 1, fig. 1, shows the general appearance of the animal and its relative size.

The brief field observations of Gilbert, in Gould (1845), made within a few years of its discovery were almost the only first-hand information on its habits for upwards of sixty years, although they contain some obviously inaccurate statements. Except for a detailed study of the general and feeding behaviour of a young animal kept in captivity for a couple of months (Fleay 1942), only a few minor original observations have since been published.

The present paper embodies the results of a part-time study which arose originally out of the author's great personal interest in the natural history of both mammals and termites, but was stimulated by the fact that the numbat is generally regarded as within sight of extinction (see, for example, Harper 1945). A better knowledge of the animal's general ecology is a prerequisite to a constructive conservation policy, and the following observations are offered as a first step towards that end.

GEOGRAPHICAL DISTRIBUTION

An attempt was made to ascertain the distribution of the numbat, both past and present, from museum specimens, the literature (including the W. Aust. Fisheries Dept. Bull. for honorary wardens), personal investigations, and discussions with naturalist friends and interested country people. In addition, some locality records were obtained from the Registers of the Western Australian Museum, relating to specimens that were received at the museum in the past, but were not preserved or have since been given to other institutions. The results of this investigation are shown on the map (Fig. 1).

There are upwards of sixty specimens with good distribution data in the world's museums. The shaded area covers the region where the numbat was living between 1954 and 1956. Because of considerations of time and pressure of other work it was not possible to investigate all areas where the animal may still occur, and it is probable that its present overall distribution is somewhat more extensive in places than that shown on the map. A considerable part of this region, however, has been cleared for farming and the animal's present distribution largely consists of a series of discontinuous areas.

The only large stretch of country from which no specimens seem to have been taken, and where the numbat occurred in the recent past (perhaps 30 years ago), is the area to the north-west of Moora and around and west of Watheroo. Supporting evidence for its occurrence there is given by Glauert's (1928) contemporary statement that " in recent years it has been reported from the Watheroo, Wongan Hills and Bencubbin districts." Numbat specimens from peripheral localities that appear to be outside its present range were collected about 30 years ago, e.g. from Kalgoorlie District (1927), Bencubbin (1928), Emu Hill, Narembeen (1926).

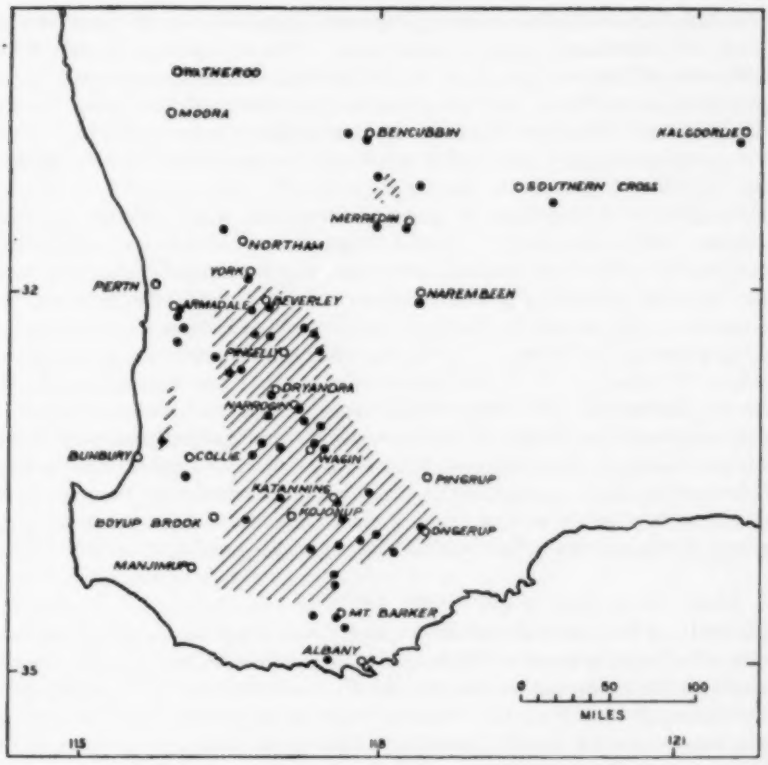

Fig. 1.—Map showing distribution of the numbat (*Myrmecobius f. fasciatus*). The full circles represent museum specimen records and the shaded area the known present-day range.

The overall distribution of the numbat has been examined in the past by Shortridge (1910) and Glauert (1933). Shortridge's map is shaded in various ways to show " ascertained present range ", " probable range ", " dying out ", and " extinct ". He gives no indication how this information was obtained. No evidence can be obtained today of the former occurrence of the numbat in a good part of the area where he indicated that it was dying out and in almost all of the area where he shows it to be extinct. For various reasons the present author considers that the numbat never occurred in the greater part of the latter area since European occupation, particularly to the east and south-east of Kalgoorlie. Shortridge, in Thomas (1907), states that the animal's range extended " very sparingly as far inland as Laverton " but he obtained no specimen in that area. An entry in an old Western Australian Museum Register records that a specimen of *M. fasciatus* registered on January 2, 1918 was received from the manager of the Ida H. mine, Laverton. The specimen was apparently in poor condition and was unfortunately not preserved. This locality is about 15 miles south and a little east of Laverton. The distribution given by Glauert (1933) was based on museum records.

The numbat's range has certainly shrunk a great deal in the past 30 years, but it is still distributed over a sizable area. The animal has not suffered the catastrophic reduction in range, or even extinction, that has happened to several other small and medium-sized mammals characteristic of this area. In some of the pockets of country where it still occurs the numbat is fairly common, and it would be true to say that it is among the more abundant of the small mammals of south-western Australia.

It might be appropriate to mention here that the "South Australian subspecies" of numbat (*M. f. rufus* Wood Jones), which has not hitherto been recorded in Western Australia, also occurs in that State. It is represented in the Western Australian Museum collection by a flat skin (M2848) registered on August 16, 1950, which was taken in the Warburton Ranges (near the common meeting point of the States of South Australia and Western Australia and the Northern Territory). It is not known whether the two forms have been in contact in historical times, but they probably inter-graded somewhere in the 500 miles between the locality of that record and the collection locality of the most easterly extant *fasciatus* specimen (Kalgoorlie District)—a distance greater than that across the known range of *fasciatus*. The characters of the animal that occurred in the Laverton area are unknown. The races differ apparently only in pelage colour, which is very variable in *f. fasciatus* and is in need of analysis.

STUDY METHODS

A study of the numbat's general biology was made in an area of about 15 square miles of woodland at Dryandra (a forestry settlement in the Narrogin district) where a population was known to occur and had been protected for many years by officers of the Western Australian Forests Department. Between September 1954 and December 1956, visits lasting from one to three days were made to the area, usually once a month. On these trips the time was divided between driving slowly along the bush roads and tracks looking for numbats, and walking through the woodland searching for numbat faeces and making observations on termite and ant abundance, possible predators, etc.

Numbats took far less notice of motor vehicles than of persons on foot, and many more were seen while driving than when walking. When an animal was sighted the vehicle was stopped and the animal was watched with binoculars. If it was disturbed and entered a hollow log, it generally reappeared within a few minutes and either continued its activities or walked slowly away, providing that no one got out of the vehicle or went near the log. Sometimes numbats were extricated from the logs for examination and marking, but usually they were not disturbed as it was desired to observe their feeding and general behaviour.

HABITAT

The study area has an annual average rainfall somewhat over 20 inches, only about 15 per cent of which falls between November and March. The summers are hot and dry and the winters are cool. Sunny days are common in winter, and there are a fair number of frosts. The climate is not of critical

importance to the numbat and there is a great variation in temperature and rainfall within its range.

The plant community comprising the study area could best be described as a mixture of shrub woodland and savannah woodland. Most of it is covered by a single dominant tree species, the wandoo (*Eucalyptus redunca* Schauer var. *elata* Benth.), which grows on clayey soils with varying amounts of sand and some pebbly laterite. The greater part of the area has a shrub understratum in which the only important species is sandplain poison (*Gastrolobium microcarpum* Meissn.) which averages about 3 or 4 feet in height. In places this shrub forms dense stands, sometimes many acres in extent. Certain other species of sclerophyllous shrubs are scattered throughout the area or are locally concentrated, depending no doubt on local soil variations. In places where the trees are much further apart the understratum consists of grass and herbs with a few scattered small shrubs.

There is a marked change in vegetation on small hills in the area on which the soil consists largely of pebbly laterite with blocks of massive laterite outcropping on the upper levels. A powder-bark (*Eucalyptus accedens* W. V. Fitz.) woodland occupies the upper parts of these hills. Although sandplain poison is a common shrub in the understratum, various other species of sclerophyllous shrubs, including several species of *Dryandra*, are abundant and may be dominant locally or over considerable areas.

Scattered throughout the area are many fallen dead trees, limbs, and branches, chiefly wandoo, or powder-bark on the laterite rises. Most of the fallen logs are hollow as a result of the activities of *Coptotermes acinaciformis* (Froggatt) while the trees were living. These logs are indispensable shelter for the numbat and it is interesting to note that the responsible termite is also its chief food item. Much of the ground surface is littered with sticks and chips and in places dead leaves of shrubs and trees. Pl. 1, fig. 2, shows numbat habitat at Dryandra.

Towards the southern boundary of the numbat's range, wandoo is partly replaced by *Eucalyptus occidentalis* Endl.; further south *E. cornuta* Labill. also appears, while towards the drier south-east *E. salmonophloia* F. Muell. enters the picture.

Immediately west of the main area of occupation of the numbat and extending to the sub-coastal Darling Range is the jarrah (*E. marginata* Sm.) forest, a typical dry sclerophyll forest, growing on lateritic soils. Jarrah is practically the only large tree in the forest, which is much less open and has much denser lower strata then the wandoo woodland. Jarrah has quite a high resistance to termite attack so that there are no hollow fallen limbs on the forest floor. The numbat does not occur in jarrah forest, which is apparently quite unsuitable for it, but it does occur in pockets of wandoo woodland on clay soil on the margins of the jarrah forest. On the western boundary of the jarrah forest, at the foot of the Darling scarp, there is a more or less continuous strip of country with clay soil covered by wandoo woodland, with some *Eucalyptus megacarpa* F. Muell. in the wetter parts towards the southern end. The numbat lives or has lived in this strip of woodland from near Bunbury in the south almost into the outer suburbs of Perth at the northern end.

From a study of the Dryandra area and a more superficial survey of other country where the numbat still occurs, it appears that the habitat requirements for the animal in south-western Australia are as follows :

(i) A woodland dominated by a species of *Eucalyptus*, the heartwood of which is eaten out by *Coptotermes acinaciformis* while the tree is living. The fallen limbs and branches provide the hollow logs required by the numbat for shelter and escape, and the food for a large proportion of the termites eaten by it. *C. acinaciformis* is the most abundant and destructive termite in south-western Australia, and over large areas practically all mature eucalypts of susceptible species are infested by it (Calaby and Gay, 1956).

(ii) Also necessary is an open shrub stratum, which seems to have a protective function for the numbat.

NUMBERS AND TERRITORY

Although the estimation of the numbat's population density was not one of the objects of the study, some relevant information was obtained. There is no doubt that the ground density is low, even in ideal habitat. Along the track where most observations were made, the greatest number of numbats seen in any one day and known from examination or, because of their distance from others, assumed to be different animals, was five, in a distance of a little over four miles. Over the most productive three-months period, during which time the area received four visits totalling six days of observation, it was considered that eight different adults and one juvenile were seen along this track. Five of the adults, two males and three females, were handled and were known to be different individuals. It is probable, however, that the number of numbats living along the transect was somewhat greater than this, perhaps as high as four per mile in the most suitable places.

In general the numbat is a solitary animal and there is reason to believe that it holds some sort of territory. It is possible that territories of males overlap those of females. Out of forty recorded sightings, two adults were seen together on only one occasion—in early April, when mating may still have been going on. Mr G. B. Sharman and others (personal communication) saw a numbat enter a hollow log on August 23, 1959. The log was found to contain two animals, a female with extended teats and a smaller but apparently adult male. A few other observations have a bearing on this point. On one occasion two adults were seen at the same time, 180 yards apart. On another occasion an adult male and an adult female were caught at places 140 yards apart on consecutive days. Twenty-one months later, a different adult male was caught at the same spot as the female. The three animals seen together on October 30 in this area, by Serventy (1954), were most probably juveniles, a conclusion supported by their extreme tameness and behaviour.

During the course of this work twelve animals were marked, either by punching small holes ($\frac{1}{8}$ inch diam.) in the ears or by carefully recording injuries to the ears or other parts of the body. Two of the ear-punched ones were subsequently recovered. An adult male was marked on April 7, 1955, and recaptured 170 yards away on October 7, 1955. An adult female was marked on July 20, 1955, and recovered on August 16, 1955, 190 yards away.

GENERAL BEHAVIOUR

One of the most interesting things about the numbat, particularly in view of its striking coloration, is the fact that it is chiefly, if not entirely, diurnal. From April to early December, numbats were seen abroad—feeding, sun-bathing, etc.—at any time of the day, but during the hot days of summer sightings were rare and only an odd one was seen early in the morning. None was seen on many trips made through the bush at night. Reliable country observers state that numbats are occasionally seen at night but such sightings are very rare. Fleay (1942) has reported that his captive never came out of its hollow log shelter at night. In some of the older literature it is said that the numbat is nocturnal ; Wood Jones (1923a) states that it is crepuscular, and Le Souef & Burrell (1926) say that it is " abroad both by day and by night ".

Fallen hollow logs are an essential feature of the numbat's habitat and it is never very far from them. When disturbed it always runs to a hollow log but not necessarily the nearest one. When removed or chased from one log it runs to another. It generally frequents long or fairly long logs with hollows of diameter 3-5 inches, but it will run into logs with large-diameter holes, or very short logs, when hard pressed. It is very difficult to extricate a numbat from the log. If grasped and pulled, it grips the wood very strongly with its claws and also presses its body very hard against the upper surface of the hollow. Other animals also used some of these hollow logs. Once a stump-tailed lizard (*Trachysaurus rugosus* (Gray)) was seen in a hollow log a little while after it was vacated by a numbat. Goannas (*Varanus gouldii* (Gray)) and rabbits were sometimes seen in or entering hollow logs in which numbats had been recorded on previous occasions. Rabbits were not very abundant in the wandoo woodland, but some of their warrens were based on large broken hollow limbs and their faeces were fairly common around some of the hollow logs known to be frequented by numbats.

Occasionally small flat nests of bark, leaves and grass were found in the hollow logs, and numbats were observed once or twice carrying bark or grass in their mouths to hollow logs. These nests are apparently not necessarily associated with breeding. Fleay's (1942) juvenile captive built a nest in its hollow log, from dead leaves and grass pulled from an old tussock with its jaws.

It is not known whether the numbat digs burrows, and no evidence of burrow digging was obtained during the present study. There is anecdotal evidence that the female digs a burrow during the breeding season. Gilbert's notebook (Whittell 1954), which contains some obvious errors, records that it breeds " in holes or short burrows ". Shortridge (1910) was told by aborigines that during the breeding season the female makes " a rather shallow perpendicular hole in the ground ". The numbat does go into holes in the ground and presumably builds nests in them. Barrett (1940) observed one enter a rabbit burrow, and subsequently dug it out. Mr L. Glauert, former Director of the Western Australian Museum, wrote in his copy of Wood Jones (1923a) (now in the museum library) that a correspondent, Mr E. C. Cecil Dival, " surprised a numbat which made for a hole in the ground. It was a burrow about three feet long at the end of which was a nest made of straw and bits of newspaper ". Glauert (1935) wrote that another correspondent, Miss

E. Wills (who donated a female and litter, which were kept alive at the museum for a time ; see later) found a litter of young in a burrow. Her dog began barking at a small hole which she dug out. After digging along for about three feet . . . " the tunnel suddenly widened from two inches into a large nesting place about nine inches in diameter, lined all around with fine dead silver grass ". In the nest were three young numbats, and a further one of the same size was found in a nearby log.

Some observations suggest that the numbat is relatively tame, but although it is sometimes possible to approach quietly quite close to an animal, in general it seems to be just as cautious and suspicious as most wild mammals. When moving about or feeding it gives the impression of being a very active and restless animal. Many of its movements are jerky and resemble similar behaviour in other small dasyurids and such placental mammals as squirrels. The normal methods of locomotion are walking and trotting. If disturbed it runs rapidly, bounding along like most mammals of comparable size. One animal was paced for a hundred yards along a track with a car and was running at a little over 20 miles per hour. Normally the tail is held horizontally or in line with the body, with the last couple of inches turned upwards slightly. Occasionally the tail may be flicked up to a vertical position or over the back and the tail hairs may be erected.

When not feeding the numbat may be observed sitting on the ground or on a fallen log. It often sits with the front legs vertical and straightened, like a house cat. The tail lies on the ground and may be straight out behind, or at right angles to the body with the tip bent a little towards the front. Sometimes when sitting up in this fashion the animal will appear to doze with the eyes partly closed, or will yawn. Yawning is quite an extraordinary procedure. The mouth is opened to a gape of 45° or so and several inches of the tongue is extruded downwards with the tip curled upwards or back towards the mouth. The mouth is then closed and the tongue slowly drawn in. Occasionally it will scratch itself on various parts of the body. An animal has been observed vigorously scratching its belly with both hands. Another was seen rubbing the back of its ears with both front paws.

The numbat also spends some time lying out or sunbasking on logs. The ventral surface of the body is flat on the log and the limbs and tail are stretched out. The animal has been seen to jump up on logs 18 inches or so in diameter to sun-bask or walk along the log. It will walk up steeply sloping dead logs but, as noted by Shortridge (1910), it does not climb trees. In some of the early literature it is stated that the numbat is arboreal. It will climb up wire-netting if hard-pressed.

Every now and again the numbat will cease feeding or whatever other normal activities it may have been engaged in, and look around, with the ears vertical and directed to the front. In this attitude it looks very alert, and it may stamp its front feet once or twice or hold up a front foot. After a few seconds it continues feeding or whatever it was doing. The holding up of a front foot is a common characteristic of the alert stance of dasyurids.

The numbat apparently does not like rain. On one occasion an observed animal was feeding when a shower of rain began. It immediately trotted to a

hollow log, smelt around the entrance for a while, and then slowly entered. On another occasion a numbat ran off when a heavy shower began and crossed a road to a hollow log, jumping over puddles about two feet in diameter on the way.

If a numbat is encountered by an observer on foot, it runs rapidly to a hollow log and enters. Usually before entering the log it stops and raises the body to the vertical and looks around. Gilbert, in Gould (1845), stated that this was an invariable procedure ; but the author has observed numbats run straight into the log without stopping.

Various reactions are displayed towards motor vehicles. If the animal is seen well ahead and is not approached too closely, it will often continue its activities as if unaware of the car. On rare occasions a numbat will behave apparently normally if a slowly moving car stops within a few feet of it. More often it will creep off slowly into the undergrowth or to a hollow log with its body close to the ground and its tail horizontal with hair erect. After it has gone a few yards in this manner it trots off with the tail raised. Sometimes it will walk or trot to a hollow log, stopping every few yards to raise the body and look around. Sometimes if one remains quiet the numbat will reappear in a few minutes and renew its feeding or other activities. More usually it comes to the mouth of the hollow log in a few minutes and, while standing in the entrance or just outside of it, gives a performance of what are apparently reactions to emotional stress. These include holding up a front paw, stamping the front feet alternately, occasionally stamping one hind foot, turning around, rapidly moving the rear half of the body up and down, and raising the body to the vertical and looking around. It looks towards the vehicle and inclines its ears in that direction. It appears very nervous and alert and all of its movements are jerky. Eventually it walks away, raising the body and looking back every few steps, until it disappears into the undergrowth. On the way it often hops up on logs, presumably to get a better view of the supposed danger. Some numbats take a long time to come out of a log when they are aware of the vehicle. The head may show within two minutes but is quickly withdrawn. This may happen several times. Eventually it will come out slowly, inch by inch, and half-an-hour may elapse before the animal comes right out of the log.

If the observer walks up to the log or shines a torch in, the numbat will not usually reappear for a long time, even up to a couple of hours. The eyes shine dull red in torchlight. As all observers have noted, a numbat extricated from a log never bites or scratches and merely attempts to escape. The animal being held in the hand in Pl. 1, fig. 1, had just been taken from a log. When a handled animal is released it may run rapidly away with the tail mostly arched up over the back and the tail hair erect. More usually it will trot or run for perhaps 10 yards, stop and look around, and then run off very rapidly with the tail up and tail hair erect. The spectacular arching of the tail and erection of the tail hair is not entirely restricted to periods of emotional stress, because it is done momentarily every now and again when searching for food or doing other normal activities.

FEEDING BEHAVIOUR

The numbat obtains its termite and ant food mostly by digging in the upper two inches or so of soil, but also by turning over sticks and other small pieces

of wood. When searching for food it walks slowly along, smelling the ground as it proceeds. It may do this for a few feet,and then walk more rapidly or trot for some distance, maybe as much as 50 feet, before smelling the ground again. As in most of its activities it appears to be very busy all the time. If food is located, or sometimes apparently when it is not, the animal digs for a while. It never seems to stay long in one place, and even when termites appear to be abundant it leaves the spot and goes on to another one. On one occasion a numbat was observed feeding for 25 minutes. In that time it dug in six places, and the area enclosed by the extreme feeding places was 3·9 acres. Another numbat was observed feeding for quite a long time. It dug in several places over a distance of about 25 yards, but concentrated on one place where it turned over about 1½ square yards of soil. A favourite feeding place is within a few feet of the bases of large wandoo trees. Here the soil is usually fairly loose and damp and contains much bark and leaf litter and also good numbers of termites. Other favoured sites are alongside partly-embedded fallen logs, partly-exposed tree-roots, and within a few feet of termite mounds. The numbat is likely, however, to find its food almost anywhere in the soil. It does not break open the mound-nests of termites. Very occasionally one will dig a few shallow pits into the top of a mound of *Amitermes obeuntis* Silvestri which has been softened by rain. Termite mounds generally are much harder than the surrounding soil, which is well populated by termites.

Having located sub-surface termite galleries by scent, the numbat squats on its hind feet and digs very rapidly with both front feet. The tongue is flicked in and out gathering up exposed termites, and the process is then repeated. Meanwhile the tail lies flat on the ground. The animal may move on a few inches and repeat the process, or it may leave the spot and trot away to begin searching for another feeding place. Occasionally only one paw will be used for digging. More rarely the animal will stand up and dig at the soil with one front foot. The numbat also turns over chips and sticks with a front foot, or with its sharp nose, or by grasping the piece of wood with its teeth. The exposed termites are then licked up. Feeding took place at any time of the day during the cooler months.

FOOD HABITS

Insects exposed by numbats that were observed feeding were collected and preserved. The prey species so obtained and their frequency of occurrence are given in Table 1.

During the course of the study a collection of numbat faeces was made, covering all months. The specimens were preserved in alcohol. Numbat faeces are generally about 7-10 mm. in diameter and 10-20 mm. long. Juvenile faeces are shorter and may be as small as 3 mm. in diameter. When fresh they are very dark brown or black in colour and have a dull glossy surface after the surface moisture has evaporated. The surface is generally smooth but may be somewhat rough if the scat contains much sand or ant remains. Usually the scats are hard, but if they contain large amounts of sand they are friable. They appear to contain little moisture when fresh. They weather to a grey

TABLE 1

Exposed insects collected from 25 numbat feeding sites, with frequency of occurrence.

	Occurrences
Termites	25
Heterotermes ferox (Froggatt)	5
Coptotermes acinaciformis (Froggatt)	5
Amitermes hartmeyeri (Silvestri)	1
A. obeuntis (Silvestri)	17
A. n. sp. (nr. *neogermanus* Hill)	1
A. sp.	2
Microcerotermes sp.	3
Termes n. sp. No. 1	2
T. sp.	1
Paracapritermes kraepelinii (Silvestri)	2
Tumulitermes apiocephalus (Silvestri)	1
T. eubaquilus (Hill)	1
Occasitermes occasus (Silvestri)	2
Ants	10
Brachyponera lutea (Mayr)	6
Rhytidoponera metallica (Fr. Smith)	1
Iridomyrmex chasei Forel (or near)	4
I. detectus (Fr. Smith)	1
Xiphomyrmex viehmeyeri Forel	1
Monomorium occidaneum Crawley (?)	1
Camponotus claripes Mayr (form " *minimus* ")	1
C. wiederkehri Forel (or near)	1
Unidentified ant (not collected)	1
Other invertebrates	1
Beetle (Pselaphid)	1

colour. Faeces were mostly found on old weathered logs, low flat-topped mounds of *Amitermes obeuntis*, and bare soil near hollow logs.

Each scat was broken up and examined thoroughly with a binocular microscope, and the prey species identified by comparison with specimens as described hereunder. Collections of termites and ants were obtained on the area during the course of the study. Worker mandible from all species of termites collected on the area were dissected out and a set of enlarged drawings made. Termites in the scats were identified generically from the worker mandibles and soldier heads and mandibles. Specific identification of termites in the scats was made by comparing the soldier jaws and sometimes soldier heads of mandibulate types, and the soldier heads of nasute species. With genera having mandibulate soldiers, sets of soldier mandibles were dissected from specimens collected locally or within 50 miles of the area, and those likely to be confused with each other were mounted on single slides ; e.g. sets of mandibles of three species of *Heterotermes* and three species of *Coptotermes* were all placed on one slide, one species of *Paracapritermes* and three of *Termes* on another slide, etc. Nasute soldiers could be compared directly so that mounting of heads was not necessary. Suitable parts of the common smaller ants were also mounted and the fragments found in scats were compared with these.

Scats consisted of termite and ant fragments mixed with a dark grey to black " ground mass " and varying amounts of sand grains. A fair number

of scats were mostly ground mass with only a small quantity of insect remains, and a couple contained no insect remains at all. Some scats consisted almost entirely of coarse sand with many fragments of ants and soldier termites.

Termites were almost always well broken up in passage through the gut although heads of both workers and mandibulate soldiers often had the mandibles still attached. Soldier heads, excluding the antennae and mandibles, of all species usually came through intact. The colour of neither termites nor ants was altered by passage through the gut. The ants were usually broken up into segments. Thoraces and nodes remained whole, and heads with mandibles still attached and gasters were common. Sometimes whole ants, usually of the genus *Monomorium*, came through with all legs and even antennae still attached. The winged reproductive castes of termites and ants were found uncommonly in the scats. Only common species were represented and there were few individuals in any particular scat.

Table 2 lists the prey species found in 252 scats (297 individual pellets), together with their relative abundance. The three categories of abundance recognized were determined by counting.

In a scat approximately 1 cm. long and 0·75 cm. diameter (a common size), a count of 1 to 5 individual insects was considered "few", 6 to 20 "moderate

TABLE 2

Prey species and relative abundance in 252 numbat scats collected at Dryandra.

	Abundant	Moderate No.	Few	Total
Termites				249
Heterotermes ferox (Froggatt)	39	52	61	152
Coptotermes acinaciformis (Froggatt)	148	39	37	224
Amitermes capito Hill	1	2	4	7
A. heterognathus Silvestri	1	1	2	4
A. modicus Hill	5	4	5	14
A. neogermanus Hill	10	7	3	20
A. obeuntis Silvestri	143	18	9	170
A. perarmatus (Silvestri)	3	1	11	15
A. n. sp. (nr. *neogermanus* Hill)	73	12	12	97
A. sp.	21	8	7	36
Abamitermes hillii Nicholls			1	1
Microcerotermes distinctus Silvestri	1	5	9	15
M. newmani Hill	2	6	16	24
M. sp.	1		45	46
Termes n. sp. No. 2		3	6	9
T. n. sp. No. 3			1	1
T. sp.			2	2
Paracapritermes kraepelinii (Silvestri)			1	1
Nasutitermes exitiosus (Hill)	1	3	14	18
Tumulitermes apiocephalus (Silvestri)	24	11	8	43
T. petilus (Hill)	1		5	6
T. subaquilus (Hill)	72	33	44	149
T. westralienesis (Hill)			1	1
T. sp.	1	3	19	23
Occasitermes occasus (Silvestri)	4	5	15	24

TABLE 2 (continued)

	Abundant	Moderate No.	Few	Total
Ants				237
Myrmecia nigriceps Mayr			1	1
Brachyponera lutea (Mayr)	3	3	23	29
Rhytidoponera metallica (Fr. Smith)	1	2	6	9
R. violacea Forel	1			1
R. sp.			3	3
Unidentified Ponerinae		2	12	14
Iridomyrmex bicknelli Emery (or near)	4	7	15	26
I. chasei Forel (or near)	8	17	73	98
I. detectus (Fr. Smith)			2	2
I. glaber Mayr	7	9	26	42
I. sp.			5	5
Meranoplus sp.			5	5
Machomyrma dispar Forel			5	5
Anisopheidole froggatti Forel	1	4	17	22
Pheidole sp.		1	2	3
Monomorium rothsteini Forel	21	23	45	89
M. sp. prob. *rothsteini*		1	3	4
M. sp. ? *micron* Crawley		2	10	12
M. sp. ? *occidaneum* Crawley			3	3
Melophorus sp.			13	13
Acropyga indistincta Crawley			2	2
Plagiolepis sp. (prob. undescribed)			3	3
Camponotus claripes Mayr (form " *minimus* ")			4	4
C. michaelseni Forel			1	1
C. nigriceps Fr. Smith (dark or " *perthiana* " form)			1	1
C. sp.			2	2
Polyrhachis sp.			2	2
unidentified ants		2	77	79
Other invertebrates				9
Beetles			7	7
unidentified arthropod ? flea			1	1
unidentified arthropod ? spider			1	1
Miscellaneous items				
hair				19
vegetable matter (rootlets, seeds, etc.)				67
charcoal fragments				55
sand grains				all

numbers ", and over 20 " abundant ". With scats of different sizes a rough calculation of the volume was made and the numbers of insects present were related to the " standard scat ".

Also analysed was a collection of six faecal pellets obtained from a specimen from Lake Muir, near the southern end of the numbat's range, which was kept in captivity for a day and then released. These faeces contained the following items ; *Heterotermes platycephalus* Froggatt—moderate number, *Nasutitermes exitiosus*—moderate number, *Tumulitermes apiocephalus*—abundant, *Occasitermes occasus*— abundant, *Brachyponera lutea*—few, small *Iridomyrmex* sp.—

few, small *Camponotus* sp.—moderate number, unidentified ants of two or three species—few, one small seed, charcoal fragments, sand grains.

In addition to the faeces, the alimentary tract of a specimen collected in the Dryandra-Narrogin area was examined. It contained the following items: *Heterotermes ferox*—abundant, *Coptotermes acinaciformis*—abundant, *Amitermes capito*—few, *A. obeuntis*—abundant, *A. perarmatus*—few, *A.* n. sp. (near *neogermanus*)—abundant, *Microcerotermes distinctus*—few, *M. newmani*—few, *Tumulitermes subaquilus*—abundant, *Brachyponera lutea*—moderate number, *Iridomyrmex bicknelli* (or near)—moderate number, *I. chasei* (or near)—abundant, *I glaber*—abundant, *Meranoplus* sp.—few, *Machomyrma dispar*—moderate number, *Anisopheidole froggatti*—few, unidentified ants of about three species—few, two small beetles, one small unidentified arthropod (probably an ant-lion larva), hair, plant stem fragments, charcoal fragments and sand grains.

There is a small overlap in the range of size and shape of the soldier mandibles of *Amitermes obeuntis* and *A. modicus*, and it is possible that an occasional occurrence of *modicus* is included in the former. A second undescribed species of *Amitermes* occurred uncommonly on the area, usually in the mounds of *A. obeuntis*. Any specimens of that species in the faeces would be counted as *A. obeuntis*. It appears to the author that it is not possible to separate *Microcerotermes newmani* and *M. serratus* (Frogg.) on isolated soldier mandibles. If any of the latter were present they would be included under *newmani*. In those scats containing more than one species of any termite genus, the number of worker mandibles was divided up in proportion to the number of soldier mandibles or heads present. This is probably not a valid procedure, but it is felt that it should give a reasonably true overall picture. In one or two cases it was possible to separate congeneric worker mandibles on size, e.g. those of *A. perarmatus* are considerably smaller than those of other *Amitermes* species present. Those termites not specifically identified were represented by worker mandibles only. A good proportion of the unidentified ants were considered unidentifiable because of the small amount of the remains.

The results of the scat analyses show that the numbat feeds largely on termites but up to about 15 per cent of the total diet consists of ants. In only seven or eight scats did ants equal or outnumber termites. There was no seasonal preference, and termites made up the great bulk of the food in all months. It is believed that these results give a true picture of the numbat's diet. A study of the soil around the feeding sites did not reveal any soft-bodied invertebrates that would leave no trace in scats.

The almost complete absence of invertebrates other than termites and ants is very striking. It seems likely that the few beetles present were inquilines, as all were very small. The sand and charcoal fragments were usually less than 1 mm. grain-size but large angular particles up to 4 mm. grain-size, or even larger were fairly common.

Termites appear to be eaten more or less in proportion to their relative abundance on the study area, taking into account that some species live in situations where it is unlikely that they would be encountered very often by the numbat. A few species of termites that occurred on the area in small

numbers did not appear in faeces, although two of these were unearthed by numbats at feeding sites. The two most important food items, *C. acinaciformis* and *A. obeuntis*, were easily the most abundant termite species on the area. The former nests within living and dead wandoo and powder-bark trees, and its galleries run out through the soil to fallen logs and other pieces of wood. A high proportion of mature wandoo trees are infested by it. *A. obeuntis* lives in mound-nests ; it is also abundant in surface soil, and attacks dead wood in contact with the ground.

Quite a different picture is obtained from a study of the ants ingested by the numbat. It is clear that the vast majority of ants eaten belong to the small species, and the species eaten in largest numbers are mostly the common predatory ones. The workers of the six species that make up most of the bulk of ants are under 4 mm. in length. Most of the *Anisopheidole froggatti* eaten were the small castes under 3-4 mm. long. *Brachyponera lutea* is somewhat larger—its workers are about 6·5 mm. long—but it is a very common ant in the favoured searching places of the numbat. (By way of comparison it might be mentioned that the soldiers of *C. acinaciformis*, the most abundant termite prey species and also among the largest, are up to 6 mm. long).

The few medium-sized and large ants eaten were apparently ingested by accident. Ants in these size-categories are common on the area. A particularly common one is *Iridomyrmex detectus*, which has workers about 9 mm. long, and which lives in large conspicuous nests. It is an aggressive ant. There were only two occurrences of this ant—a single individual in one scat and four in the other. Medium-sized and large castes of *Camponotus* species, which are non-aggressive, are common but their remains were rare in the faeces. All except one of the few taken were the smaller species or smaller castes. A few winged females of *Brachyponera lutea*, which are about 10 mm. long, were eaten. An interesting item was a single worker of *Myrmecia nigriceps* found in one scat. This large ant is about 20-25 mm. long, is very aggressive and has an extremely painful sting. The individual found would certainly have been eaten by accident.

There is no doubt that termites are much the favoured food of the numbat and it seems probable that it does not deliberately search for ants. When termites are exposed, however, most ants—particularly *Iridomyrmex* species—will run in and seize them and carry them off. In such circumstances the ants are eaten by the numbat. In digging for termites the numbat may also break into ants' nests or galleries. In the twenty-five feeding sites examined (Table 1), termite galleries were exposed in all, but ant galleries in only four of the ten sites where ants were present. The presence of ant cocoons in six of the scats (18 in one case) also testifies to the fact that ants' nests are broken into. The cocoons in three of the scats were almost certainly those of *Rhytidoponera metallica*. It is possible that the numbat may search for a few species of ants such as *Monomorium rothsteini*, which was very common in the scats, although considerably less abundant than several termite species. However, small *Monomorium* species often live in deserted termite nests or galleries, and are found in dense clusters in their nests. Because of the low population density of the numbat and its methods of feeding, it is self-evident that it would have

no effect on the populations of termites and ants, nor even on individual termite colonies and probably also ant colonies.

The numbat appears to swallow most if not all of its food without chewing. Fleay (1942) states that his captive subjected the large (10-15 mm.) soldiers of *Neotermes insularis* (Walker) to " rapid and audible mastication " ; but it is to be noted that no termites with soldiers of anywhere near this size occur within the natural range of the animal. There were very few individual ants in this size range among the very large number of ants that were found in the scats. In view of the large amount of angular sand-grains ingested, tooth wear could be expected to be excessive if the numbat regularly chewed its prey ; but an examination of the molar teeth of museum specimens shows that this is not the case. Moreover, the degenerate nature of the teeth and the extraordinary dental anomalies (Bensley 1903 ; and unpublished data) strongly suggest that the pre-molars and molars are not used and are therefore not being subjected to selection pressure.

There is little objective evidence in the literature on the diet of the numbat. The best observations are those of Fleay (1942), who presented his captive with a variety of foods including termites, ants and their eggs, various beetles and beetle larvae, earthworms, raw eggs, bread and milk, honey and jam. The animal showed an overwhelming preference for termites and Fleay concluded that the numbat is " practically entirely " a termite-eater. The animal ate " odd ants' eggs and some ant larvae and cocoon-enclosed pupae, but only when hungry ". Mr A. M. Douglas (personal communication) has kept numbats in captivity on a couple of occasions. His captives were fed on termites and would not eat ants when presented with them. He formed the opinion from his observations that the numbat ate ants only incidentally and when feeding, may even be worried by ants. Mr Douglas' observations also led him to the belief that the numbat prefers *A. obeuntis* to other termite species. A note in an old Western Australian Museum Register, referring to a numbat specimen, states " . . . white ants found in stomach ". Another note in the same register regarding another specimen records that it was kept alive for several days and would eat raw beef but not mutton, and " did not seem to care for ants ". Tate (1951) and Troughton (1954) give prominence to Fleay's work and state that the numbat prefers termites from wood. (In southern Victoria, where Fleay worked, termites are much less abundant than in the numbat's natural range, and the only places where they can be found in quantity are in old rotting tree stumps.) Shortridge, in Thomas (1907), records one stomach " full of white ants, most of which had evidently been swallowed whole ".

Other published statements on the numbat's diet are based on surmise or anecdotal evidence. Le Souef & Burrell (1926) state that it lives on termites. Barrett (1940) states that termites are its favourite food, and " ants are not to their liking, but they do not feed exclusively upon termites according to careful observers of numbat ways ". Gould (1845), who obtained his information from Gilbert and Grey, thought that ants or their larvae probably made up the bulk of its food but stated that he had no direct evidence. He also believed that it fed " upon honey and a species of manna which exudes from the

leaves of the Eucalypti ", but does not indicate where he obtained this remarkable information. In Gould's plate a numbat is depicted taking large ants (approximately 11 mm. long) from the undisturbed ground surface around the ants' nest. It is the present author's belief that such a situation does not occur in nature. Gilbert (Whittell 1954) " never found anything in the stomach but white ants " and considered these " their exclusive food in a state of nature ". He would certainly have passed this information on to Gould, and it is known that he sent at least thirteen numbat specimens to Gould (Glauert 1950).

From the fact that the type specimen was collected in country that " abounded with decayed trees and ant-hills " and also because of the anatomical peculiarities of the animal, Waterhouse (1836) concluded that it lived " chiefly, if not wholly, upon ants ". Lydekker (1894) states that Waterhouse's inference " has been fully confirmed by actual observation ", and that the numbat will " also eat insects of other kinds, and even, it is said, grass." It must be pointed out that Gould and other early naturalists did not distinguish between ants (Hymenoptera, Formicidae) and termites or " white ants " (Isoptera), and called both these unrelated groups " ants ".

BREEDING

Examination of captured females provided some information on breeding, which is presented as Table 3. Supplementary data on breeding was obtained from the several litters of pouch young in the collection of the Western Australian Museum, but unfortunately they have only dates of registration and no collection dates. It could be expected that for most of the litters the registration date would approximate to the collection date, but the data are unreliable.

All of the registration dates and young sizes fall within the range of those obtained in the field in the present study, except for two specimens that were registered in February, and a litter that was collected in June. One of the February specimens, a filled skin of an adult female (M974), has a note on the

TABLE 3

Breeding data on female numbats

Date	Breeding Condition	Crown-rump Length of Young (approximate only)
March 26	4 young	very small
May 30	4 young	25 mm.
June 2	4 young	30 mm.
June 19	2 young	40 mm.
July 17	2 young (1 male, 1 female)	55 mm.
July 20	4 young (2 males, 2 females)	60 mm.
Aug. 23	all four teats extended, not examined for lactation	
Sept. 2	lactating in 3 teats	
Sept. 2	lactating in 4 teats	
Sept. 3	non-breeding	

label reading "with three young in pouch". This skin has every appearance of having been fresh when prepared and does not appear to have been kept in spirit. A letter from the donor, dated 8th February, 1928, preserved in the museum files, gives the impression that the specimen was freshly caught, as the donor was in a hurry to despatch it. Entered in the Register opposite a specimen (M1704) registered 1st February, 1934, is a note reading " 3 young attached ". There seems no doubt that this specimen had been fresh as it was received from the zoological gardens and the above note is written in ink over a pencilled note reading " alive at zoo ". Unfortunately the size of the young is not known as neither litter seems to have been kept. The litters were not given Registration numbers and cannot now be found in the collections. The latter litter, and probably also the former, would have been born at least as early as January.

Also in the Western Australian Museum are specimens of four litter mates (M1868 and M1871-3), which were received with the mother on June 19 (" caught 16.6.34 ") and kept in captivity for some time. When received they were " about 3/4 in. long " (Glauert *in litt.* to Troughton 1954). This litter would have been born at least a month later than any recorded in Table 3.

There are indications of a seasonal cycle of fertility in the male. Mr G. B. Sharman (personal communication) took a testis from an adult male in the Dryandra-Narrogin area on 3rd September. He also examined the testis of an adult male collected in the Bannister area on 19th May. In both specimens he found numerous mitotic divisions but no meiosis, and no mature sperms could be found in either testis.

It appears then that the numbat has a definite breeding season, and that copulation must take place from mid-summer to early autumn (December to perhaps April) and the young are born in summer to autumn or early winter (January to April or May). The young are carried or nursed by the mother through the winter and some young at least are foraging on their own account in October. The only statement in the literature on the breeding of the numbat is Wood Jones' (1923a) remark. " The breeding season in Western Australia is in June and July, and four young constitute the normal litter."

GROWTH OF YOUNG

The only information on the growth-rate and length of pouch life of the young numbat is provided by the litter of four mentioned previously, that were captured on 16th June, 1934 when the young were " about 3/4 inches long " (i.e. about 20 mm.), and were kept in captivity for about three months at the Western Australian Museum. However, with regard to growth rate, the data are not very reliable as the lengths of the young when captured are known only approximately and the young died after a time. One died on 28th August when its approximate crown-rump length was 53 mm. and the others died between 18th and 21st September, when their head-and-body lengths were 78, 79, and 80 mm. Their eyes had recently opened and they had only recently become detached from the teats, and were still generally attached to the mother (A. M. Douglas, personal communication). Wood Jones (1923b) examined a litter of four of approximate head-and-body lengths of 75 mm.

He commented on the fact that they were relatively large and far advanced, but the condition of the lip margins was such that their liberation from the teats would not take place in the near future.

The Western Australian Museum litter would have been at least a month old when captured so that the pouch life is at least of four months duration, and the total nursing period probably as long as six months. This is a long pouch life and slow development when compared with marsupials of comparable size. For example, Fleay (1934, 1935) observed that the dasyurids, *Phascogale tapoatafa* (Meyer) and *Dasyurus quoll* (Zimmermann), somewhat smaller and considerably larger respectively when adult, than the numbat, detached from the teat at about 66 days of age, and their eyes were first seen open in 89 days and 11 weeks, respectively. He considered that the young of these species were capable of independent existence at about 4 and 4½ months of age respectively. Hill & Osman Hill (1955) have confirmed Fleay's results for *D. quoll*. They found that the young first detaches from the teat from about seven weeks to two months of age, the eyes are open in about three months, and the animal is able to fend for itself at the age of 4 to 4½ months.

The numbat's growth after detachment from the teat is probably rapid and it probably breeds in its first year. Animals that were obviously juveniles were seen abroad foraging in October, November and December, but none were seen in the field after summer.

The female has no pouch and the young are firmly attached to the teat by their mouth and also hang on tightly by their hands to the long hair of the " pouch area ". If touched, the already curled bodies curl up even more and the hands grip the hair even more tightly. In any litter the young may all be of one sex or any combination of both sexes. The external characters of the pouch young have been described by Wood Jones (1923b), who comments on the remarkable difference in general appearance between young and adult, particularly with regard to the " pug dog " face of the young. The colour of the hair on his specimens has apparently faded with preservation, as seems to happen to all very young numbats, or indeed numbats of any age, preserved in spirit. Some observations on colour of the young were collected in the field in the present study. The youngest to show hair were the 30 mm. specimens, which were clothed with a thin golden down, particularly on the fore half. The 40 mm. young were covered with short sandy-coloured down and no bands were visible. Dark bars on the rump were barely visible on the 55 mm. young, and dark and light bars were showing well on the 60 mm. specimens.

The three young of head-and-body lengths 78-80 mm. are preserved in the Western Australian Museum as filled skins (M1871-3). They are well furred. Dorsally the fur is a light reddish-brown, liberally interspersed with longer white hairs, for more than half-way down the back, to the beginning of the dark bars. The dark bars on the rump are dark-brown with a slightly reddish appearance. The pale bars are cream or very pale reddish-brown. The tail hair is golden-brown or pale reddish-brown, both above and below. The fur on the face is a light reddish-brown, similar in colour to that on the back, with many white hairs particularly from the nose to about the position of the ears. The dark stripe through the eyes is well developed. Ventrally the fur

is white or creamy white. The colour of the young *M. f. fasciatus* contains much more red than that of the adult and resembles more the colour of the adult *M. f. rufus*.

ADULT WEIGHT

Several adult males were weighed with the following results : 500 g. (March) ; 495 g. (April), and same animal in following October 550 g ; 550 g. (May) ; 455 g. (June) ; 377 g. (July) ; 530 g., 503 g., (September). Because of the appearance of the fur, scarred ears, and large testes, the light animal was considered to be adult. Unfortunately no females were weighed without pouch young. Three females with pouch young had the following weights : 474 g. (four young, 30 mm., June) ; 610 g. (four young, 60 mm., July) ; 430 g. (two young, 55 mm., July). The weights of the young were assumed to be roughly the same as other marsupial pouch young of the same dimensions, and when subtracted gave the following approximate weights for the three females : 450 g., 530 g., 400 g. The only published weights of the numbat are those of Finlayson (1947). He obtained approximate weights from preserved material of known history and applied a correction obtained from the loss of weight undergone by similar specimens weighed in the field when fresh and having a similar history of preservation. He obtained a weight of 293 g. for an adult male from the Narrogin district, and 347 g. for a South Australian desert adult female of *M. f. rufus*. The weight of the *fasciatus* specimen is certainly much too low and that of the *rufus* specimen also no doubt somewhat low.

VOICE

When the numbat is handled or disturbed in its hollow log, both sexes often produce a low throaty growl, with the mouth closed. All observers have remarked on this sound. Gilbert, in Gould (1845) described it as " a sort of half-smothered grunt, apparently produced by a succession of hard breathings ", while Fleay (1942) described it as " low-toned churring noises of protest that could be likened to sounds of heavy breathing ". Both sexes also utter a series of rapidly-repeated hissing sounds, usually when being handled. These sounds are quite loud and are produced with the mouth open. This hissing sound is much like similar sounds produced by many species of marsupials. A further sound produced by the numbat is reported by Fleay (1942) who heard once ' a rapid and very Phascogale-like series of " tut-tut-tut-tuts ! " '

PREDATORS

Many possible predators were seen on the area but no evidence was obtained that they killed numbats. They were the domestic dog, the domestic cat (tame and feral), the fox (*Vulpes vulpes* (Linn.)), several species of hawk, the goanna (*Varanus gouldii* (Gray)), and the carpet snake (*Morelia variegata* (Gray)). Except for at least two pairs of little eagles (*Hieraaëtus morphnoides* (Gould)), which were resident on the area, hawks were rarely seen. Other species that could kill a numbat were the wedge-tailed eagle (*Aquila audax* (Latham)), the goshawk (*Accipiter fasciatus* (Vigors and Horsfield)), the square-tailed kite (*Lophoictinia isura* (Gould)), which were seen once or twice only,

and possibly the brown hawk (*Falco berigora* Vigors and Horsfield), which was seen a few times. Hawks were watched closely but the only records of prey were the following : a goshawk was seen perched and holding a fairly large skink ; a brown hawk was seen carrying a small brown mammal, almost certainly a mouse (*Mus musculus* Linn.) ; a little eagle was observed eating a rabbit kitten. On one occasion two little eagles were disturbed from a tree under which was found a regurgitated pellet, containing a few dark feathers and a great mass of fur of a rat-kangaroo (*Bettongia penicillata* Gray). Unfortunately no nests of hawks could be found. As the numbat is usually to be found around old logs, or in shrubby country, or under trees, it is thought that it would not be seen or hunted much by hawks, with the probable exception of the goshawk.

House cats in the area occasionally killed rabbits and mice, rarely a bandicoot (*Isoodon obesulus* (Shaw)), and on one occasion a brush-tailed phascogale (*Phascogale tapoatafa* (Meyer)). None brought home any numbats although they were fairly common and lived close to the Dryandra settlement. One record was obtained of a dog killing a numbat, in the district, but not on the study area. Foxes were seen occasionally at night and one was disturbed close to a young possum (*Trichosurus vulpecula* (Kerr)) at the base of a tree. About thirty fox scats were collected on the area, mostly on nesting mounds of the mallee fowl (*Leipoa ocellata* Gould), but none contained remains of the numbat or other native mammals. They were mostly composed of rabbit remains, sheep wool, and invertebrates, chiefly beetles. A note in a Western Australian Museum Register states that a specimen was " killed by a fox ". The evidence for the alleged killing (which almost certainly was not observed) is not stated, and a search in the museum files did not produce any correspondence with the donor of the specimen. The diurnal behaviour of the numbat probably protects it from the fox (and maybe also from the cat). Foxes are sometimes seen hunting in daytime, but they are largely nocturnal predators. Numbats living or sheltering in holes in the ground would be vulnerable to fox predation if discovered.

Goannas were fairly common and sometimes went into hollow logs in which numbats were observed on previous or subsequent occasions. Carpet snakes or their sloughed skins were rarely seen. It is thought that these reptiles are more likely to be predators on the numbat than other animals listed, as they enter the hollow logs. It should also be mentioned that numbats are occasionally killed by motor vehicles along the main roads that traverse areas where it still occurs.

PARASITES

Ten numbats were searched for ectoparasites but few were found. Two animals harboured mites, one mite in one case and seven in the other. The mites were in the short sparse hair around the scrotum and were actively moving about. They were identified as *Mesolaelaps australiensis* (Hirst) by Domrow (1958). This mite has a wide host range. Ticks were found on four animals, one having two and the others one each. They were attached to various parts of the body. They were indentified by Mr D. C. Swan (personal communication) as *Ixodes vestitus* Neumann and *I. holocyclus* Neumann.

The former is usually associated with the numbat but has been recorded rarely on other hosts, and the latter was also found on other hosts (macropodids) in south-western Australia. Mr Swan also has specimens of *Amblyomma triguttatum* Koch (as defined by Robinson (1926)) taken from the numbat. This is the common " bush tick " of south-western Australia and has a wide host range. No lice or fleas were found, but two species of flea (*Echidnophaga myrmecobii* Rothschild and *E. perilis* Jordan) have been recorded from the numbat. Both species have a wide host range (Hopkins & Rothschild, 1953).

One alimentary tract from a numbat collected in the Dryandra-Narrogin district was examined for internal parasites. Some minute nematodes from the stomach were identified as an undescribed species of Trichostrongylidae by Mackerras (1958). This is the only recorded internal parasite of the numbat.

MISCELLANEOUS OBSERVATIONS

Three of the males examined had had one or more small pieces torn from the margins of the ears at some time. One male had a large scab, 12 mm. in diameter, on the body under the foreleg. The hair had fallen out around the wound, which was healing well. One female, which had two young on the belly, had lost one of its hind feet at some time, and the injury had healed completely.

Two males examined had a strong smell which was very similar to the odour of wet unwashed dogs. The smell seemed to be strongest in the pre-sternal gland area. An area around the gland, about 15 mm. in diameter, was bare of hair in both cases and in one case it was slightly swollen and reddish and was stained orange-brown on the anterior margin of the gland. Other males examined had pre-sternal glands bare of hair but did not have the " doggy " smell. The gland is present in both sexes and may be bare or largely covered with hair. Also the hair around the general area of the gland may or may not be stained orange-brown.

CONSERVATION

The numbat's range has shrunk a great deal since the beginning of settlement in Western Australia, and the animal has disappeared from large parts of the overall area it now occupies. The chief reasons that have been advanced for the decline include clearing of land, bush fires, and the introduced predators —domestic dog, cat, and particularly the fox (Harper 1945, Le Souef & Burrell 1926, Troughton 1954).

It is the author's belief that the role of the predators in the numbat's decline has been much over-rated. As suggested previously, the fox is probably not important as it hunts mostly at night when the numbat is not active and is confined to its hollow-log shelters. Foxes and cats are abundant in all areas where the numbat is still fairly common. Wild fires would certainly clear the numbat from the burnt area, but such fires are so rare nowadays in the woodland where the numbat lives as to be of little importance. Slow controlled burning, as it is performed in normal forestry practice, appears to be of little practical significance. It is done on small areas and mostly burns the sticks, grass, and litter and does not harm the trees or sound hollow logs.

Numbats have been seen foraging on areas where sticks and animal dung were still smouldering. The termite populations in the soil are also largely unharmed by controlled burning of the woodland floor.

It is considered that the clearing of land for farming purposes is the only real danger to the continued survival of the numbat. Complete clearing removes it entirely. It persists well in bush blocks that are left, and even appears able to stand a certain amount of clearing of the woodland floor, for some time at least ; but the fallen hollow logs are of crucial importance and the numbat disappears with these. Land clearance is progressing at an increasing rate.

The future of the numbat can only be assured by the provision of adequate reserves. Ideally these should be large as the animal has a low density and the minimum breeding population that will persist indefinitely is unknown. There should also be several such reserves to avoid possible harmful genetic effects in small populations. Perhaps a more important reason for having a number of reserves in different areas is that in southern Western Australia there is evidence of environmental changes that have had a profound effect on mammal distribution and abundance (Main 1959). Several species of mammals became extinct in historical times before the invasion of the rabbit and the fox and before agricultural development had taken place in large areas of the State. Other species, the bones of which are found in the superficial layers in limestone caves, became extinct in recent times but prior to European occupation.

There are a number of reserves, mostly small ones, in which the numbat occurs, and in which wildlife is protected. The primary purpose of the majority, if not all, of these is not fauna conservation, and they are controlled by various Government Departments. Some are reserved for forestry purposes, others are water-catchments, etc. To avoid conflict of interests an adequate number of suitable reserves for rare fauna should be set aside under the control of the State fauna authorities. Such reserves would give sanctuary to many things beside the numbat. In the woodland around Dryandra (most of which is a forest reserve under the control of the Forests Department, the rest being a railway water-catchment under the control of the Railway Department) the following other species of native mammals were recorded during the course of the present study ; echidna (*Tachyglossus aculeatus* (Shaw)), brush-tailed phascogale (*Phascogale tapoatafa* Meyer), bandicoot (*Isoodon obesulus* (Shaw)), pigmy possum (*Cercaërtus concinnus* (Gould)), possum (*Trichosurus vulpecula* (Kerr)), honey mouse (*Tarsipes spenserae* Gray), brush-tailed rat-kangaroo (*Bettongia penicillata* Gray), tammar (*Protemnodon eugenii* (Desmarest)), brush wallaby (*P. irma* (Jourdan)), grey kangaroo (*Macropus ocydromus* Gould). The future of some of these is by no means secure. Another area was found in the Brookton district that harboured several species of native mammals, including the numbat and brush-tailed rat-kangaroo. The latter is a rare animal nowadays.

For the effective conservation of the numbat and other wildlife in reserves, it is self-evident that there should be no clearing of the shrubs and logs and litter on the woodland floor. The chief problem likely to arise is that of rabbit control, as the presence of rabbits on reserves is a constant source of embarrassment for Government authorities. The rabbit does not occur in great numbers

in most of the woodland where the numbat occurs, but it is still the most abundant mammal. For effective rabbit control the logs and litter would have to be cleared, which would be fatal for the numbat. Also it would be unwise to fumigate rabbit burrows as they are known to be used by the numbat. Poisoning would jeopardize the survival of the rat-kangaroo and other macropodids and the possum. Perhaps little could be done about the rabbit beyond controlling it in buffer zones between reserves and farming-land. It would probably be possible to control the fox if necessary by laying baits in such a way that the possibility of their being taken by carnivorous marsupials would be low.

Farmers who have unimproved " bush paddocks " that are likely to remain uncleared could play an important part in the conservation of the numbat and other native mammals. In fact some farmers in south-western Australia already encourage and rigidly protect wildlife on their properties, even mammals such as the kangaroo that are regarded as pests by many landholders.

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Fig. 1.—Adult male numbat held in the hand. (Photo by G. M. Dunnet.)

Fig. 2.—Numbat habitat at Dryandra, W. Aust. The trees are wandoo (*Eucalyptus redunca* var. *elata*) and the shrubs are sandplain poison (*Gastrolobium microcarpum*). (Photo by A. R. Main.)

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ON THE RESPIRATION OF AQUATIC HEMIPTERA HETEROPTERA WITH SPECIAL REFERENCE TO THE CORIXIDAE

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(With 19 figures in the text)

Aquatic Hemiptera Heteroptera have ventrally placed anterior thoracic and abdominal spiracles, the posterior thoracic and first abdominal spiracles being situated dorsally. Internally the spiracles are joined by paired thoracic and abdominal longitudinal tracheal trunks. Gas bubbles carried on the body surface function as gas stores and physical gills. In the Naucoridae, Nepidae and Notonectidae gas store replenishment occurs posteriorly and the main inspiration air currents enter the first abdominal spiracles from under the wings (Naucoridae) or the posterior abdominal spiracles (Nepidae) or via the ventral abdominal surface (Notonectidae). Gas is expired from the anterior thoracic spiracles (Naucoridae and Notonectidae) or the posterior abdominal spiracles (Nepidae). These water bugs are predaceous amongst aquatic vegetation and obtain their main supply of oxygen by ventilation of the tracheal system, while surfacing. In contrast, the Aphelocheiridae are permanently submerged and use a plastron respiration. The Corixidae are bottom livers. The longitudinal abdominal tracheal trunks are vestigial, gaseous exchange being restricted mainly to the thoracic region. Gas is expired from the anterior and posterior thoracic spiracles on to the ventral and dorsal abdominal surfaces respectively and here gaseous exchange take place between the air bubbles and the water. Inspiration takes place through the first abdominal spiracles. Corixids are normally negatively phototactic, but become positively phototactic when deficient in oxygen. Gas store replenishment occurs anteriorly by momentary contact with the air water interface and is associated with specialized mating habits. The large gas stores make the insect very buoyant and the specialised method of locomotion is associated with this.

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INTRODUCTION

The Pterygota originally evolved as terrestrial animals, but a number of families have subsequently invaded aquatic conditions. The Hemiptera have probably colonised fresh water on more than one occasion and modern species occur in most types of habitat. The Gerridae and Veliidae, respectively, occur on stagnant and running waters, the Notonectidae wait for their prey just below the surface, while the carnivorous Naucoridae and Nepidae occur amongst submerged vegetation. The Corixidae are mainly bottom dwellers ; a mode of life, which has led to great modifications of body structure. Contrary to the views of Sutton (1951), primitive carnivory has been replaced by algal and detritus feeding (Popham unpublished), while special methods of respiration have evolved to give submerged insects a continuous oxygen supply. This in turn is associated with modifications of the locomotory and mating habits.

The invasion of aquatic conditions presents special respiratory difficulties. Many terrestrial adephagan Coleoptera have a pair of convex, non-overlapping elytra and the dorsally placed abdominal spiracles open into the subelytral cavity. This organisation is easily adapted to aquatic conditions. In the Dytiscidae and other aquatic Coleoptera, the subelytral cavity acts both as an air store, during submergence, and as a connection between the tracheal system and atmosphere for tracheal ventilation during surfacing. Many of the Hygrobiidae, Dytiscidae and Gyrinidae posteriorly extrude, from beneath the elytra, a small gas bubble which functions as a physical gill (Ege 1915). In these Coleoptera, the abdominal sternites are thick and laterally strengthened, while the tergites are thin and comparatively flexible. By means of a well developed abdominal musculature, which gives the insect a globular form, gas is pumped to and fro, through the subelytral cavity, between the tracheal system and the extruded gas bubble. Many of the aquatic Adephaga carry no air on the abdominal surface, though in the Haliplidae the gas under the hind coxal plates also functions as a physical gill (Hickman 1931). In many terrestrial Hemiptera Heteroptera, such as the Pentatomidae and Coreidae, a different organisation exists. The abdominal spiracles are ventral. The flat overlapping flexible hemi-elytra normally lie over the dorsal side of the abdomen and the subhemielytral space is less valuable as a gas store than in Coleoptera. Aquatic Hemiptera Heteroptera have no simple means of connecting the abdominal tracheal system with the atmosphere during surfacing. Notonectids have overcome this difficulty by swimming dorsal side downwards and in having the

ventral abdominal spiracles, on each side of the body, situated between two rows of hydrofuge hairs, enclosing a gas space connecting the tracheal system with the atmosphere during surfacing. In the Nepidae and Belostomatidae the atmosphere is connected by the posterior respiratory tube with the tracheal system through the posterior abdominal spiracles.

The Corixidae have a neater and simpler solution to this respiratory problem. The hydrofuge body surface is largely surrounded by a series of gas bubbles, which function as a physical gill and provide the main oxygen supply, while the insect is submerged, the superficial gas stores being rapidly replenished by momentary contact with the water-surface.

Amongst the aquatic Hemiptera Heteroptera, the respiration and tracheal system of *Aphelocheirus aestivalis* Westwood has been described by Thorpe & Crisp (1947-1949), of *Nepa cinera* L. by Dogs (1912) and Hamilton (1931), and of *Ilyocoris* (*Naucoris*) *cimicoides* Stål by Kramer (1935) and Wrede & Kramer (1926). Rawat (1939) has given an accurate account of the anatomy and morphology of *Ilyocoris cimicoides*, while Hoppe (1912) has given a full account of the external morphology of *Notonecta*, though a published account of the tracheal system is lacking. In view of the differences in the interpretation of Brocher (1909) and Hoppe (l.c.) on the functions of the notonectid spiracles, the respiration of *Notonecta* needs reinvestigation. The work of Ege (1915) and of De Ruiter *et alii* (1952) has shown the surface gas stores of *Naucoris*, *Notonecta* and *Corixa* function as physical gills. An account of the functional morphology of the structures associated with respiration in *Corixa* would fill a useful gap is existing knowledge and, with additional matter on *Ilyocoris* and *Notonecta*, make it possible to survey the respiration of aquatic Hemiptera Heteroptera, and provide a morphological basis for future experimental studies. It is with these matters this paper is concerned.

THE RESPIRATION OF *CORIXA PUNCTATA* (Illig.)

Adult respiration.

Body form (Fig. 1)

In British species of *Corixa*, the body is dorso-ventrally flattened and the sclerotised hemielytra are folded over the dorsal wall of the abdomen. The head is opisthognathous, being convex anteriorly and concave posteriorly, and attached by a short narrow neck to the convex front wall of the prothorax. This segment (Fig. 1, PT) is likewise convexo-concave, in longitudinal section, and is joined by a short narrow peduncle to the ptero-thoracic segments (Fig. 1, T). This gives the head a wide range of movement for food collecting. The pronotum (Fig. 1, PN) is greatly elongated and forms a dorsal shield over the front of the pterothorax. The pterothoracic segments are inclined forwards. Each segment is composed of a tergum (divided into subsidiary sclerites), a small sternum, and the sides are formed from the enlarged pleural sclerites, which extend upwards above the edges of the terga, leaving on each side a large mesothoracic lateral pouch (Fig. 3a, LP), extended posteriorly as a shallow metathoracic lateral groove (Fig. 3a, LG). The lateral groove ends just in front of the anterior abdominal spiracles, and the groove lips are slightly flexed downwards. When the wings are folded over the abdomen, the lateral flange of

the hemielytron (Fig. 1, LFE) forms a roof to the groove and pouch. Anteriorly, the pouch is closed by the folded first and second auxillary wing sclerites (Fig. 3a, AS). A lateral depression on the underside of the hemielytron catches in a small dorsal peg at the pleural junction of the meso- and meta-thorax. An anterior flange of the clavus fits into a transverse groove (Fig. 7, TG) along the rear end of the mesothorax. The front wings (or hemielytra) are sclerotised

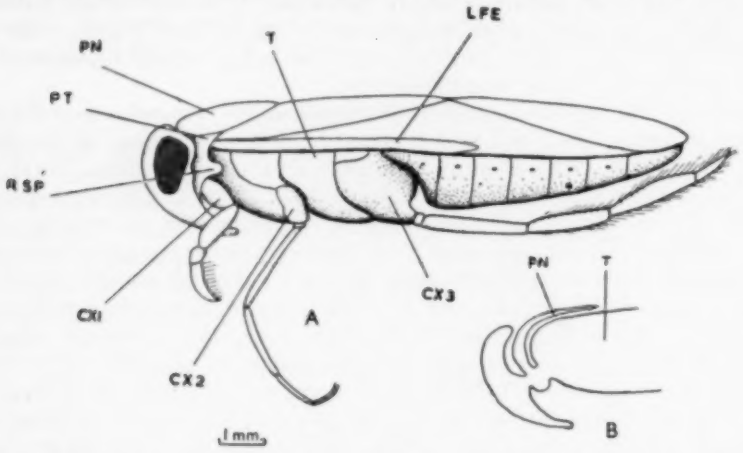

Fig. 1.—*Corixa punctata*. A. Lateral view. B. Median section through anterior end. CX 1 Prothoracic coxa ; CX 2 Mesothoracic coxa ; CX 3 Metathoracic coxa ; LFE Lateral flange of hemi-elytron ; PN Pronotum ; PT Prothorax ; RSP Rectangular shaped process ; T Pterothorax.

and composed of a clavus, corium and membrane. The hind wings are membranous and normally folded longitudinally over the abdomen, the folded auxillary wing sclerites lying in a depression between the lateral groove and the metatergum. The small specialised front legs are used for feeding in both sexes and in the males also for stridulation and holding the female during copulation. The middle legs are unspecialised except for the long claws, which anchor the insect to the substratum when feeding.

The hind limbs are used for swimming and have large posteriorly directed coxae (Figs. 1 and 2, CX3) situated close to the mid line and extending inwards and backwards under the ventral surface of the abdomen. These coxae accommodate the large leg muscles, used for locomotion. The abdominal segments are dorso-ventrally flattened, and each has a narrow tergum and sternum. The front of the abdomen is laterally and ventrally constricted to provide room for movement of the hind legs (See Fig. 1). The female genitalia are posteriorly situated, but in the male the genitalia are displaced laterally to the left in *Corixa punctata* (Illig.) and related species or to the right in most other British species. The significance of this asymmetry will be discussed later.

The superficial gas stores

The corixid body surface is strongly hydrofuge. When the insects are submerged, gas bubbles collect in surface depressions, occuring between the

head and prothorax, between the prothorax and the pterothorax and extending posteriorly over the lateral flange of the hemielytra, under the pronotum and hemielytra, between the folds of the hind wing, as well as on the under side of the abdomen. The gas bubbles are held on the concave dorsal abdominal

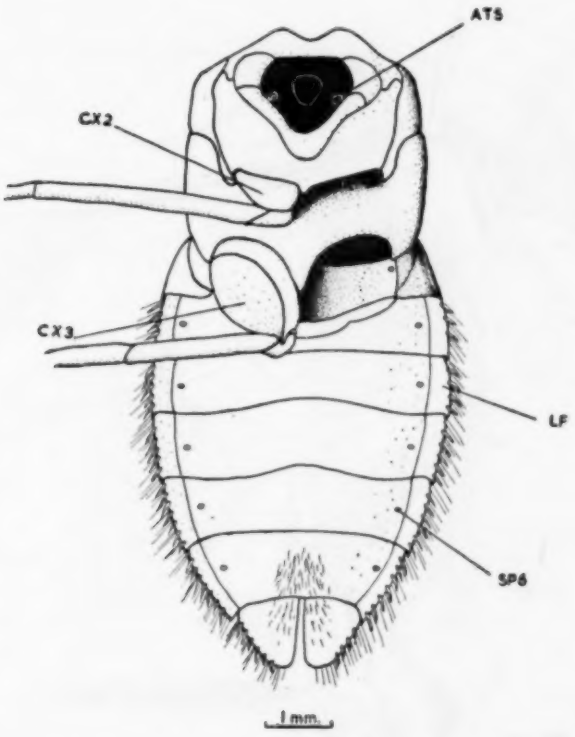

Fig. 2.—*Corixa punctata*. Ventral view of pterothorax and abdomen. ATS Anterior thoracic spiracle ; CX 2 Meso-thoracic coxa ; CX 3 Meta-thoracic coxa ; LF Lateral flange to abdomen ; SP 6 Sixth abdominal spiracle.

surface by lateral flanges (Fig. 2, LF) edged with hydrofuge setae. Gas stores also occur between the coxae, and in the depression between the thorax and abdomen. The dorsal and ventral gas stores are connected by lateral gas stores between the head and prothorax, between the prothorax and pterothorax, between the pterothorax and the abdomen.

Tracheal system (Figs. 3, 4 and 5)

The anterior thoracic spiracles (Fig. 2, ATS) are situated ventrally in the arthrodial membrane between the pro and meso-thorax. The posterior thoracic spiracles (Fig. 3, PTS) and the first abdominal spiracles (Fig. 3, sp. 1) are situated laterally on each side of the dorsal surface. The remaining six pairs of

abdominal spiracles are smaller, being situated ventro-laterally on segments 2 to 7 inclusive (Fig. 2, sp. 2-7). On each side, the posterior thoracic spiracle

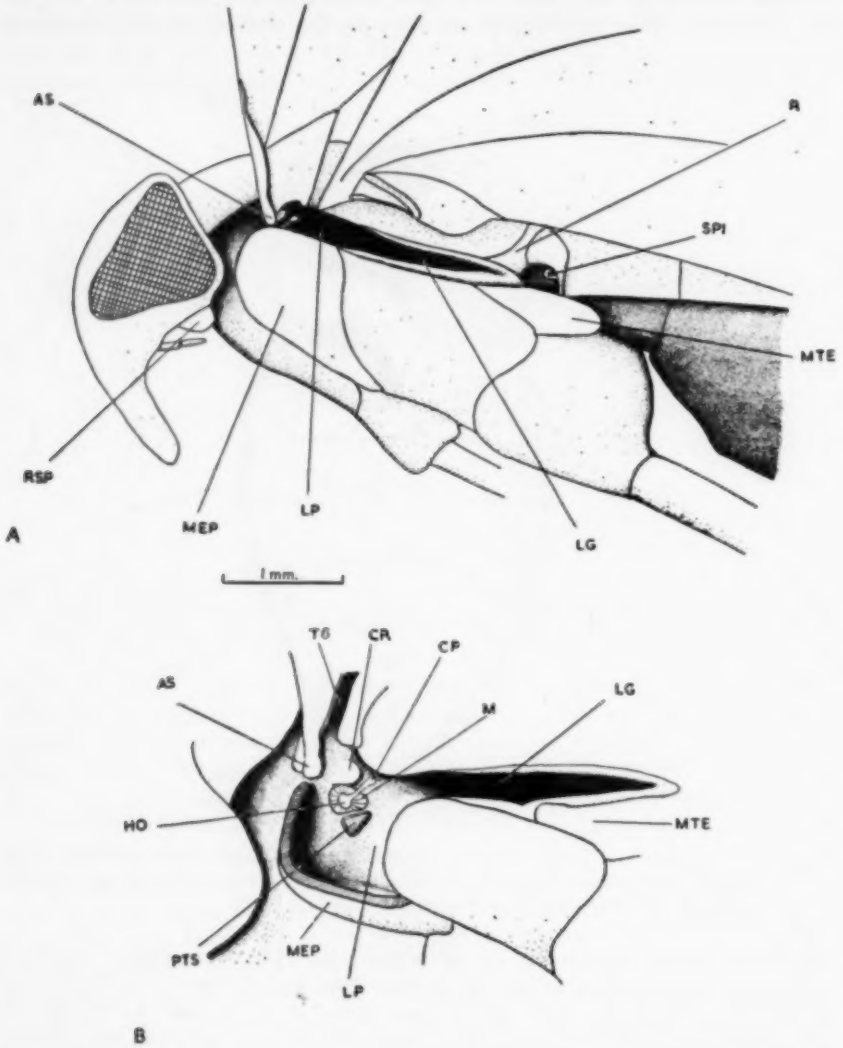

Fig. 3.—*Corixa punctata*. A. Lateral view of head and thorax to show lateral pouch, lateral groove and first abdominal spiracle. B. Lateral view of lateral pouch with greater part of the mesepimeron cut away. AS Anterior auxiliary wing sclerites ; CR Cuticular ridge ; CP Clubbed process ; HO Hagemann's organ ; LG Lateral groove ; LP Lateral pouch ; M Membrane ; MEP Mesepimeron ; MTE Metepimeron ; PTS Posterior thoracic spiracles ; R. Ridge ; RSP Rectangular shaped process ; SP 1 First abdominal spiracle ; TG Transverse groove.

(Fig. 3b, PTS) occurs immediately ventral to the base, in a lateral pouch (LP) formed between the body wall and the mesepimeron (MEP). The lateral pouch can be connected with sub-hemielytral space by the lateral groove (LG), between the body wall and the meta-episternum (MTE). Normally, however,

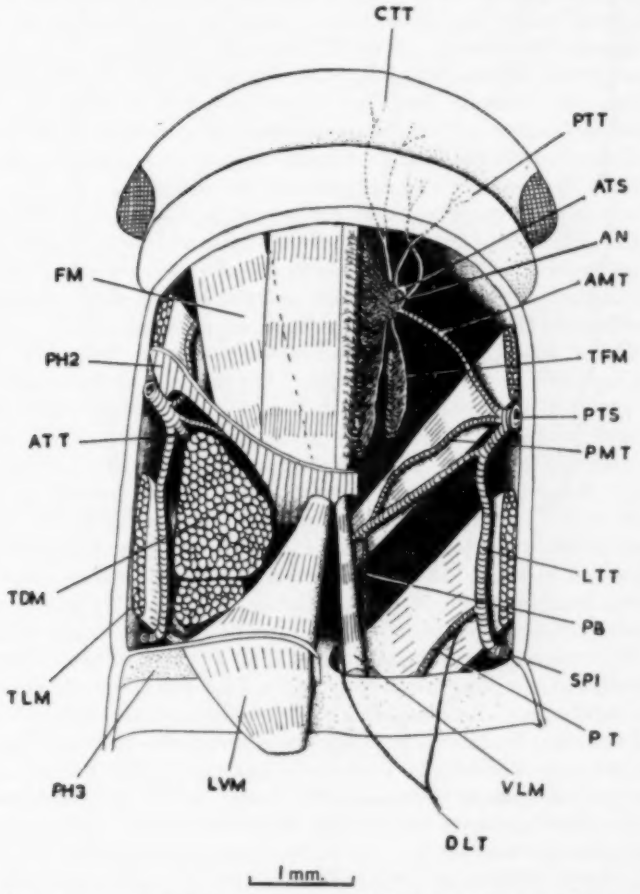

Fig. 4.—*Coriza punctata*. Dorsal view of the head and thorax. The pterothorax is dissected to show the thoracic tracheal system. On the right side the second phragma has been cut away and the dorsal muscles have been removed. AN Tracheal anastomosis ; AMT Anterior mesothoracic tracheal trunk ; ATS Anterior thoracic spiracles ; ATT Anterior metathoracic trunk ; CTT Cerebral tracheal trunk ; DLT Dorsal longitudinal tracheal trunk ; FM Flight muscles ; LTT Lateral tracheal trunk ; LVM Longitudinal ventral muscles of first abdominal segment ; PB Posterior branch of ATT ; PH 2 Second phragma ; PH 3 Third phragma ; PMT Posterior mesothoracic tracheal trunk ; PT Posterior metathoracic tracheal trunk ; PTS Posterior thoracic spiracle ; PTT Prothoracic tracheae ; SP 1 First abdominal spiracle ; TDM Trochanter depressor muscles ; TFM Tracheae to flight muscles ; TLM Trochanter elevator muscles ; VLM Ventral longitudinal muscle of metathorax.

the connection is closed by a slight ridge (R) on the dorsal thoracic surface, immediately anterior to the first abdominal spiracle. The anterior abdominal spiracle is situated laterally in arthrodial membrane between the metatergum and the first abdominal tergite. This spiracle is connected by an air space, mesad to the metepisternum with the dorsal and ventral abdominal gas stores.

On the inner wall of the lateral pouch, immediately in front of the posterior thoracic spiracle Hagemann's organ (HO) occurs.

Compared with *Locusta*, which shows a relatively primitive pterygote thoracic organisation, the thoracic segments slant forwards, causing the coxae to be directed backwards. These changes bring the anterior thoracic spiracles (ATS) into the ventral position, and raise the first abdominal spiracles to lie latero-dorsally between the metatergum and the abdomen.

Each anterior thoracic spiracle gives rise to a cervical tracheal trunk, (Fig. 4, CTT), which runs forwards and divides into two on entering the head, and to a lateral branch, which runs forwards dorsally into the prothorax (Fig. 4, PTT). Posteriorly, the anterior thoracic spiracle sends a short tracheal branch to an anastomosis (Fig, 4, AN) of tiny tracheae, situated ventral to the flight muscles (Fig. 4, FM). From this anastomosis numerous fine tracheae (Fig. 4, TFM) run upwards to the flight muscles. The anterior thoracic spiracle leads into the anterior mesothoracic trunk (Fig. 4, AMT) which runs backwards, upwards and outwards, mesad to the coxal muscles of the middle legs to the posterior thoracic spiracle. The posterior mesothoracic trunk (Fig. 4, PMT) runs mesad from the posterior thoracic spiracle, downwards and slightly backwards, to the mesothoracic coxal muscles and the middle legs. On each side, a large lateral tracheal trunk (Fig. 4, LTT) joins the posterior thoracic and first abdominal spiracles and lies between the metathoracic coxal muscles. The anterior tracheal trunk of the metathorax (Fig. 4, ATT) arises just behind the posterior thoracic spiracle and then runs downwards, inwards and backwards to the ventral longitudinal muscles (Fig. 4, VLM) of the metathorax, as well as giving rise to a posterior branch (Fig. 4, PB), which runs down the median side of the hind coxa. Besides giving rise to many small tracheae, which supply the coxal muscles, the lateral tracheal trunk gives off a posterior branch (Fig. 4, PT), which runs downwards, backwards and inwards to the hind legs. The thoracic tracheal system is functionally more or less self-contained having only slight connections with the tracheae of the abdomen. The dorsal abdominal longitudinal tracheal trunks (Fig. 5, DLT) are exceptionally thin and almost vestigial. Each abdominal longitudinal trunk is joined anteriorly to the thoracic tracheal system by a pair of thin tubes. One branch joins the posterior tracheal trunk of the metathorax just below the lateral tracheal trunk, and the other branch runs medially forwards to the mesothoracic tracheal anastomosis described above.

The tracheae of each abdominal spiracle (Fig. 5, sp. 2-7) do not make any obvious connection with those from the opposite side if the body, nor are they connected with tracheae of adjacent segments, except by means of the thin dorsal longitudinal trunks already mentioned.

The tracheae from the second and third abdominal segments run inwards to the laterally situated gonads (GN), but also send a few fine tracheae to the

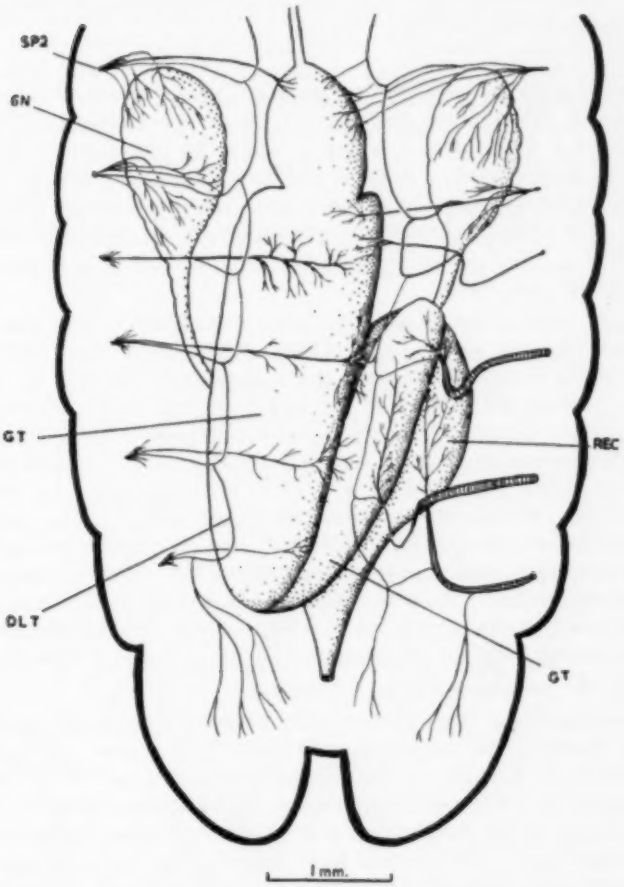

Fig. 5.—*Corixa punctata*. Dorsal view of the abdominal tracheal system. DLT Dorsal longitudinal tracheal trunk ; GN Gonad ; GT Mid Gut ; REC Rectum ; SP 2 Second abdominal spiracle.

ventral side of the gut. The tracheae from the 4th to 7th spiracles (inclusive) run mainly to the gut (GT). In *Corixa punctata*, the gut is S-shaped and the midgut (GT), hindgut and rectum (R) are displaced to the right side. Associated with this feature, the tracheae from the 5th, 6th and 7th spiracles on the right side run first medially backwards and then forwards to supply the dorsal side of the midgut and hindgut. The anterior region of the rectum is mainly supplied from the 7th abdominal spiracle on the right side. The tracheae from the 4th, 5th, 6th and 7th spiracles on the left side are thinner than most abdominal tracheae, whereas those on the right side are better developed. This asymmetry of the gut and associated tracheal tubes occurs in both sexes.

This simplification of the abdominal tracheal system is secondary and not

primitive, being due to lack of development of the longitudinal abdominal trunks and associated tracheae.

Spiracles

The anterior thoracic spiracles are protected by a rectangular shaped process (Figs. 1 and 3A, RSP) on the posterior margin of the prothorax. The thoracic spiracles have a short atrium, which is closed by paired lips. The lips are equal in size in the anterior thoracic and first abdominal spiracles, but in the posterior thoracic spiracle, the anterior lip is appreciably larger than the posterior lip. The abdominal spiracles have a short atrium, the inner end of which can be closed.

Function of the gas stores

Although various functions have been attributed to the gas stores by previous authors, the work of Ege (1915), of Thorpe & Crisp (1947-1949), of De Ruiter *et alii* (1952) and Popham (1954) has established that the main function of the surface gas stores is to act as a " physical gill ". During submergence, oxygen, withdrawn from the gas stores, is replaced by diffusion of the gas from the surrounding water. In a similar way, carbon dioxide passes from the insect into the gas stores later to dissolve in the water by virtue of its high solubility. Within certain limits the oxygen supply in the gas stores can be continuously replenished as long as sufficient nitrogen is present ; but the reduction of oxygen tension automatically raises the nitrogen tension and this gas, therefore, gradually dissolves, passing out of the gas stores into the water. When the gas bubbles shrink below a critical size, the means of obtaining oxygen is removed and an oxygen deficiency is produced within the insect.

Changes in the gas stores during submergence

Because there is a high contact angle between the cuticle and the water, there is a resistance to the movement of gas bubbles over the body surface. The resistance on the outer surface of the gas bubbles, at the air-water interface, is negligible. For these reasons the superficial gas stores are not easily moved over the insect surface and also have a glutinous appearance. When first submerged most of the corixid body surface is covered with superficial gas stores, which then gradually contract over the dorsal and ventral abdominal surfaces towards the thorax, in extreme cases, the ventral gas stores being reduced to small bubbles round the bases of the metathoracic coxae. While these changes take place, gas appears under the pronotum and between the pro-and mesothoracic legs. This gas is subsequently moved backwards, by the hind legs, along the underside of the body, until the gas stores are once more evenly distributed over the ventral abdominal surface.

It is possible that the accumulation of gas under the pronotum and round the thoracic leg bases may be due to surface irregularities, or similar mechanical factors ; but a small gas bubble, on the end of a pipette, placed against the pronotal edge is rapidly incorporated into the surface bubbles and the abdominal gas stores dilate at the expense of those of the thorax. Therefore, the increased gas appearing under the pronotum can only have been expired from the anterior thoracic spiracles. In addition, gas appearing between the wings and the dorsal thoracic surface can only have been expired from one or both pairs of dorsal

spiracles. The slight ridge, on each side, between the posterior thoracic and anterior abdominal spiracles acts as a barrier to the movement of gas. The hind legs are, therefore, rubbed backwards over the body, and gas is forced under the wings into the dorsal abdominal gas stores. To do this, the hind legs are flexed over the back until the tibia and tarsi are transverse. In this position, the ventral side of the limb segments is in contact with the dorsal body surface. This region of the hind limbs bears a longitudinal row of obliquely set strong setae (Fig. 6, DS and VS). As the leg is moved backwards over the body surface, the setae press on the elytra and drive the gas stores posteriorly under the hemielytra. A similar set of setae on the dorsal side of the limb segments are used to move the gas stores on the ventral side of the abdomen.

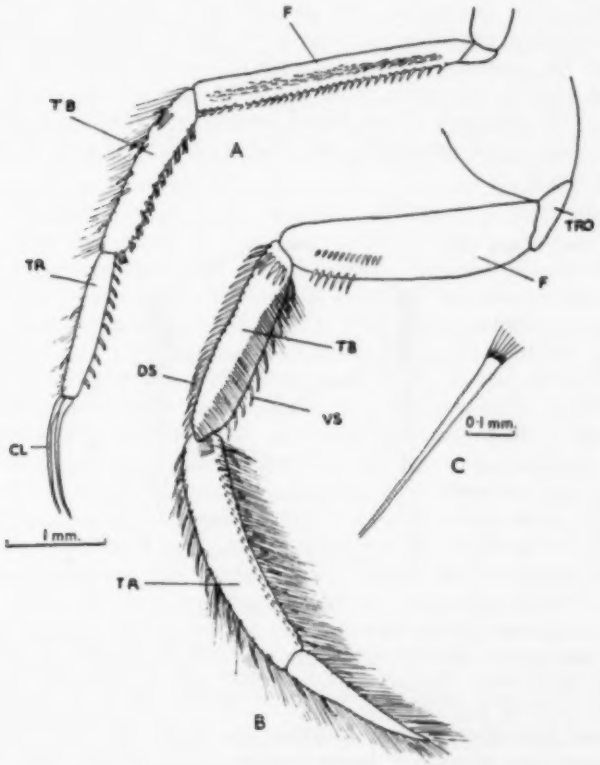

Fig. 6.—*Corixa punctata*. Posterior views of the meso- and metathoracic legs. A Mesothoracic leg ; B Metathoracic leg ; C Spatulate hairs on base of tibia of metathoracic leg. CL Claws ; DS Dorsal setae ; F Femur ; TB Tibia ; TR Tarsus ; TRO Trochanter ; VS Ventral setae.

The tibiae (Fig. 7, TB) and tarsi (TR) of the hind legs may also be moved longitudinally to and fro against the sides of the abdomen, and the gas bubbles are then pushed backwards, while held between the dorsal and ventral limb

setae, which are also situated round the base of the tibia, to form a shallow basket-like structure (Fig. 6). As the legs are extended along the sides of the abdomen the dorsal gas stores are caught between these setae and the bubble is moved backwards under the hemielytra : the abdomen sometimes being bent downwards to facilitate these gas movements. When the legs are pulled forwards, the hydrofuge setae are withdrawn from the bubble edge, the gas tending to remain in its new position. Contraction of the longitudinal ventral muscles of the first abdominal segment (Fig. 4, LVM) depresses the abdomen and thus helps to draw gas towards the posterior end of the abdomen. The dorsoventral flattening of the abdomen increases the surface area of the gas stores and facilitates gaseous exchanges between the bubbles and the surrounding water. The subsequent shrinkage of the dorsal abdominal gas stores can only be explained on the assumption that gas is mainly absorbed through the first abdominal spiracles, the ridge (R), mentioned above, greatly reducing inspiration through the posterior thoracic spiracles. There can be little doubt that some of the ventral gas stores enter the body through the other abdominal spiracles, but the fine bore of the dorsal longitudinal tracheal trunks suggests that the amount of gas passing between the thoracic and abdominal tracheae is relatively small.

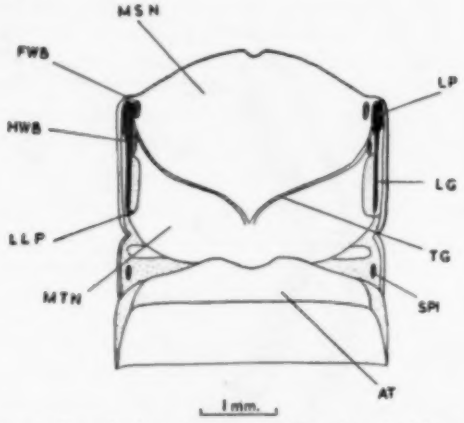

Fig. 7.—*Corixa punctata*. Dorsal view of thorax after wings had been removed. AT First abdominal tergite ; FWB Front wing base ; HWB Hind wing base ; LG Lateral groove ; LLP Longitudinal lateral pocket ; LP Lateral pouch ; MSN Mesothoracic notum ; MTN Metathoracic notum ; SPI Anterior abdominal spiracle ; TG Transverse groove.

Compared with the thoracic muscles, the abdominal organs have a low energy output and, therefore, lower oxygen consumption. Whether all gas expired from the abdomen leaves the body by the thoracic or abdominal spiracles—or both—is not known, but the thorax is certainly the main centre of gaseous exchange and the respiration of the abdomen can, for practical purposes, be more or less ignored.

The abdominal musculature of *Corixa panzeri* (Fieb.) has been described by Larsen (1945) and there can be little doubt these muscles aid tracheal ventilation as in other insects.

While settled on the bottom, corixids sometimes twitch the middle legs towards the body, where upon gas appears under the prothorax. Similarly, Botjes (1932) has shown that the accumulation of carbon dioxide in the gas stores stimulates flexure of the hind legs and a current of oxygenated water is swept over the abdominal gas stores—a process which occurs automatically while the insect is swimming. De Ruiter *et al.* (loc. cit.) describe similar fanning movements in *Notonecta* and *Naucoris* in high carbon dioxide tensions. These leg movements are sometimes also accompanied by expiration of gas under the prothorax and may, therefore, be used to aid the ventilation movements. The dorsal surface of the pterothorax is composed of an anterior mesonotum, which medially is posteriorly extended (Fig. 7, MSN). The second phragmata (Fig. 4, PH2) form a vertical dorsal sheet of cuticle, between the meso- and metathorax and which is ventrally attached, by muscles, to the furcal processes. The second phragmata act, therefore, as a median brace between the meso- and metanota and between the pleura on each side of the thorax.

Anteriorly, the metanotum is attached to the second phragmata and posteriorly to the third phragmata (Fig. 4, PH3). Laterally, the metanotum is attached to the pleura by thin strips of cuticle at the anterior and posterior corners—the remainder of the lateral margin of the sclerite being attached to arthrodial membrane which forms lateral longitudinal pocket (Fig. 7, LLP), one on each side, into which the auxillary sclerites of the hind wings are folded, when the wings are flexed over the abdomen. The movements of the hind legs towards the body during " abdominal fanning " are due to the contraction of the trochanter depressor muscles (Fig. 4, TDM), which originate on the metanotum. Contraction of these muscles causes a depression of the metanotum. If the anterior thoracic spiracles are open at this time, gas would be expired. When the legs are extended sideways owing to the contraction of the trochanter levator muscles (Fig. 4, TLM), the metanotum returns to its original position by virtue of its elasticity. Gas could be drawn into the pterothorax, if the first abdominal spiracles were then open. It seems likely that the circulation of gas over the body surface and the ventilation of the pterothorax occurs automatically while the insect is swimming. Unfortunately this is difficult to observe, but it is significant that corixids made to swim continously for several minutes in a current of water, invariably maintain an even distribution of the gas stores on the body surface. It is, of course, possible that during swimming gas enters and leaves the pterothorax by the same spiracles, but this is a matter for further investigation. The functional advantage of passing gas forwards through the thorax and backwards over the body surface, instead of the reverse directions, would seem to be that gas is easily moved backwards over the body surface, while the animal is swimming, but could not be moved forwards against surface water currents.

Surfacing causes

In 1910 Hagemann described a specialised sense organ (Fig. 3b) immediately in front of the posterior thoracic spiracle. This organ consists of an oval membrane bearing a club-like structure, in the base of which Hagemann described a number of scolophore cells. Just in front of the club-like process

(CP) is a cuticular ridge (Fig. 3b, CR) shaped like an escarpment : the steep side being posterior and bearing numerous fine setae. A fuller account of the organ and its function will be given elsewhere (Popham, unpublished). Although Hagemann's suggestion that the organ has an auditory function cannot be easily disproved, there is evidence that when corixids swim to depths ranging from 10 to 25 feet the increased hydrostatic pressure causes water to enter the sub-hemielytral space, and move forwards over the mouth of the lateral groove and pouch, to push the clubbed process against the cuticular ridge, and stimulate surfacing. An organ capable of warning the insect that its tracheal system is in danger of flooding has, therefore, considerable survival value. Organs of this kind have already been described for *Nepa* (Baunache 1912) and *Aphelocheirus aestivalis* (Thorpe & Crisp 1949).

Hagemann's organ is situated in the lateral pouch containing gas at a constant volume, irrespective of the movements of gas over the body surface, described above. The anterior pouch probably functions as a trap to keep water away from the spiracles.

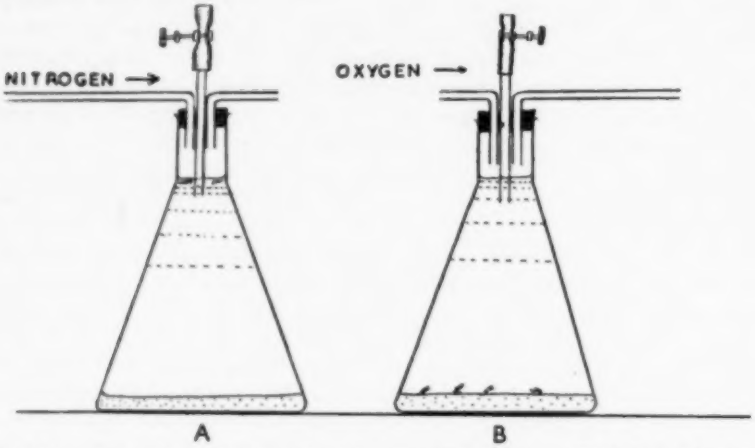

Fig. 8.—Apparatus used. Flask A contains nitrogen saturated water. Flask B contains oxygen saturated water.

Botjes' (1932) observation that an increase of pressure causes corixids to surface has been confirmed. This surfacing factor does not operate in shallow water, nor while the insect retains a residue of gas stores on the surface, and another operative surfacing factor must, therefore, exist. Increased pressure also reduces gas store size and thus the combined buoyancy of the insects and their gas stores. It is possible a decrease of buoyancy may cause corixids to surface but the following experiments suggest otherwise. Using a 500 cc. conical flask (Fig. 8a) lined with sand, three parts filled with nitrogen saturated water at 18°C, closed with a rubber bung and with a stream of nitrogen, containing a trace of oxygen (sufficient to keep the insects moving) passed through the gas space. Ten specimens of *Corixa germari* were introduced into the flask through a special tube, normally closed by rubber tubing fitted with a pinch

cock. Under these conditions the insects surfaced on an average every 22 seconds (2,000 surfacing), during which period a negligible amount of nitrogen could dissolve from the gas stores. De Ruiter *et al.* (l.c.) record a similar phenomenon in *Naucoris*. In a second experiment, using oxygen in place of nitrogen, both as the gas and in solution, the insects surfaced on the average after 14 minutes (350 surfacings), by which time the surface gas stores had almost disappeared and the insects had become denser than water. From these two experiments it would appear that it is not loss of buoyancy or lack of nitrogen so much as lack of oxygen, which causes surfacing.

Another possible surfacing factor is the presence of carbon dioxide. Many aquatic Coleoptera and Notonectidae surface for several minutes, while the tracheal system is ventilated, whereas corixids make only a momentary contact with the atmosphere, during which time the gas stores are rapidly replenished and the opportunity for removing carbon dioxide from the tracheal system must be negligible. Moreover the high solubility of the carbon dioxide and the circulation of gas through the thorax make it unlikely that carbon dioxide accumulates in the gas stores to any appreciable extent. Although the influence of this gas may be small, it is reasonable to assume the main surfacing factor is oxygen deficiency. De Ruiter *et al.* (loc. cit.) found increases of carbon dioxide tension in the gas stores decreased the amount of time *Notonecta* spent at the surface and had little or no effect upon the surfacing frequency.

Normally, surfacing corixids either float or swim with the body inclined upwards to the air-water interface, with the head, thorax and abdomen in line. On touching the air, the head and prothorax are bent downwards, so that the pronotum is raised from the bases of the hemielytra. As the general body surface is strongly hydrofuge, water retires from the gap between the pro- and pterothorax and air rapidly enters the superficial gas stores. The insect then returns to the bottom, excess gas escaping from the tip of the abdomen.

The efficiency of this method of gas store replenishment depends upon the speed with which the junction of the pronotum and wing bases can be exposed to the air and the slowness with which the water returns. Ideally the pronotal and hemielytral cuticles should have high advancing and retreating angles when wetted. Holdgate (1955) has shown that aquatic insects with a rough surface have advancing angles exceeding 150 degrees and retreating angles of comparable magnitude.

In the larger corixids, such as *Corixa punctata* and related species, the cuticular surfaces of the pronotum and hemielytra are smooth, but in the smaller species various degrees of cuticular roughening occurs. In *C. linnei* (Fieb.), *C. sahlbergi* (Fieb.) and related species the pronotum is rastrated, being raised into a large number of transverse and a few longitudinal ridges, but the cuticle of the hemielytra remains smooth. The pronotum is raised against the movement of water over the body surface and there is, therefore, a greater functional need for the pronotum (rather than the hemielytra) to be rastrated. In most of the smaller British species of *Corixa*, both the pronotum and corium of the hemielytra are rastrated. The surface rastration is particularly valuable in the smaller corixids, where the pronotum is small and the insects are in contact with the atmosphere for a shorter period. While it is true to say that

none of the larger species of corixids is rastrated and very few of the smaller species have not both the pronotum and hemielytra rastrated, there is no close correlation between the size of the species and the degree of rastration. Thus *Corixa affinis* Leach has a smooth pronotum and hemielytra, whereas *C. carinata* (Sahl.) and *C. germari* (Fieb.), which are slightly longer (though also narrower) have a rastrated pronotum and hemielytra. Similarly small species such as *C. lateralis* Leach or *C. castanea* (Thom) have a rastrated pronotum, but smooth hemielytra, whereas *C. distincta* (Fieb.) and *C. falleni* (Fieb.), which are three millimetres longer have rastrated front wings. The rastrated dorsal surface also acts as a trap for small gas bubbles as the insects brush against submerged vegetation or against the under side of the ice in winter. Air bubbles trapped in this way are incorporated into the general surface gas stores by the movements of the hind legs described below.

Reversal of phototactic reactions.

In the dark corixids are guided to and from the surface by the stimulus of gravity and/or the buoyancy of the gas stores. In the light, surfacing must occur as quickly as possible to reduce predatory attacks to a minimum. It might be expected, therefore, that corixids, and perhaps other bottom living water insects, might use light stimuli to guide them to and from the surface.

To investigate this possiblity, it is necessary to separate the directions of buoyancy-thrust from the direction of illumination. This can be done by directing a parallel beam of light from the side of the aquarium slightly downwards on to the water surface ; the rays being refracted obliquely towards the bottom at minimum angle of 40 degrees to the vertical (Fig. 9a). If corixids are neutral in their light reactions, they would, while surfacing under these conditions, take a more or less vertical path between the bottom and the surface on both journeys (Fig. 9a (i)). They would, however, take an obliquely inclined path either towards or away from the light according to whether they were positively or negatively phototactic. When twenty specimens of *Corixa dorsalis* Leach were tested under these conditions it was found that out of 150 surfacings only ten were 10 degrees or less from the vertical and the other 140 paths were inclined *towards* the light. On returning to the bottom the insects swam obliquely towards light on three occasions, 15 paths were vertically downwards and the remaining 132 paths were inclined *away* from the light. A typical path to and from the surface is shown in Fig. 9a (ii). When the aquarium was illuminated from below, through a clearing in the sand, corixids in the dark surfaced taking vertical paths on both journeys, but corixids entering the light turned and swam downwards towards the bottom. *Corixa punctata* (Illig.), *C. linnei* (Fieb.), *C. praeusta* (Fieb.) and hydroporid beetles showed similar reversals of phototactic responses and the problem therefore arises as to the cause of this phenomenon.

It has been shown above corixids are positively phototactic, while surfacing owing to a deficiency of oxygen, but become phototactic soon after the gas stores have been replenished and the oxygen deficiency presumably removed. Corixids might reasonably be expected to show similar reversals of phototactic reactions in other situations. When migrating from one habitat

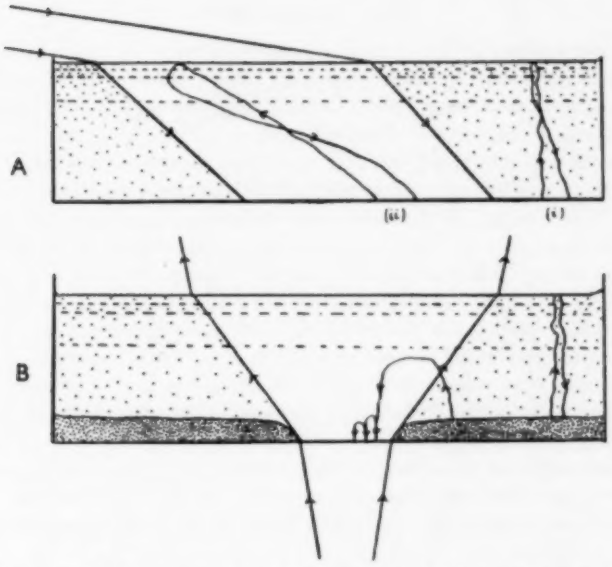

Fig. 9.—A. Diagram of an experimental tank lit from the side giving an obliquely directed beam towards the bottom. Path (i) shows the course taken by an insect in the dark. Path (ii) shows the course taken by an insect in the oblique beam.
B. Diagram of an experimental tank lit from beneath. Path (i) shows route taken by an insect in the dark. Path (ii) shows the route taken by an insect entering the divergent beam.

to another, corixids sometimes fly from the water surface. Here they first orientate themselves away from light, but turn towards it when the wings vibrate. The initial flight path is towards the light, unless modified by other factors, notably wind. Sometimes surfaced corixids vibrate their wings for only a few seconds orientating themselves towards light, while the wings are moving, but turning away from light when wing vibration stops. This phenomenon first observed in the laboratory (Popham 1942) has subsequently been observed many times also in the field (Popham 1953), when several species of corixids and water beetles behaved in this way.

The work of Krogh & Weis Fogh (1915), of Raffy & Portier (1931), of Chadwick (1947) and Chadwick & Gilmore (1940) shows insects absorb more oxygen in flight than at rest. Chadwick (loc. cit.) and Chadwick & Gilmore (loc. cit.) showed that *Drosophila* produced an oxygen debt, which lasted for several minutes after flight ceased. If corixids behave similarly, it is reasonable to assume wing vibration is associated with an oxygen debt, which disappears after the wings stop moving, and confirms the suggestion corixids are normally negatively phototactic, but become positively phototactic when deficient of oxygen.

Fig. 9a shows reversal from positive to negative phototaxis occurs soon after leaving the water surface. This implies oxygen must quickly reach the organs controlling the orientation to light, but this is a matter for further investigation.

Nymphal respiration

As the respiration of the nymphs resembles that of the adults in many respects, it is sufficient to summarise the main points of difference. In the first and second instars respiration is cutaneous, though the tracheal system is already formed (Fig. 10). From the anterior thoracic spriacles arise small tracheae which run into the head, thorax and by means of two dorsal longitudinal trunks to the abdomen ; a lateral longitudinal trunk supplies the thorax.

In the third instar the thoracic and abdominal spiracles are open. The pronotum is short and the wing pads are dorso-laterally situated on the pterothorax. Hydrofuge hairs on the anterior and lateral edges of the pterothorax and wings (Fig. 11) hold gas bubbles between the body surface and the developing wing buds. Into these gas bubbles open the posterior thoracic and first abdominal spiracles. Gas is also carried on the ventral surface of the body. In later instars the respiratory diffusion distances are gradually increased due to a thickening of the cuticle and increased size causing a reduction in the body surface/volume ratio. This is compensated by increase in the size of the wing pads and associated gas stores, gaseous exchanges occuring more easily through the gas-water interface of the gas stores than the cuticle. Between the first nymphal instar and the adult, there is a gradual increase in the size

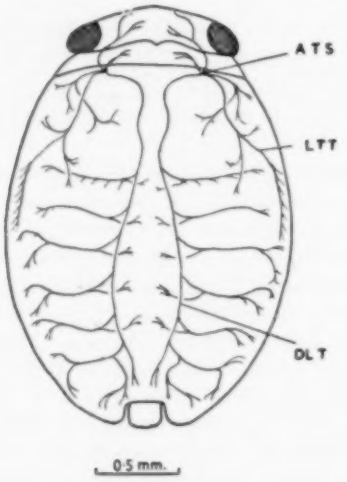

Fig. 10.—*Corixa punctata*. Dorsal view of the first instar showing nymphal tracheal system. ATS Anterior thoracic spiracle (situated on ventral surface) ; DLT Dorsal longitudinal tracheal trunk ; LTT Lateral thoracic trunk.

of the lateral thoracic trunks ; the abdominal longitudinal trunks remaining thin and vestigial in the adult.

The form of the tracheal system of Corixidae has enabled the insects to leave the surface and colonise a variety of bottom habitats. These modifications of the respiratory organs have in no way reduced thoracic ventilation during flight, and corixids readily migrate from one habitat to another. The

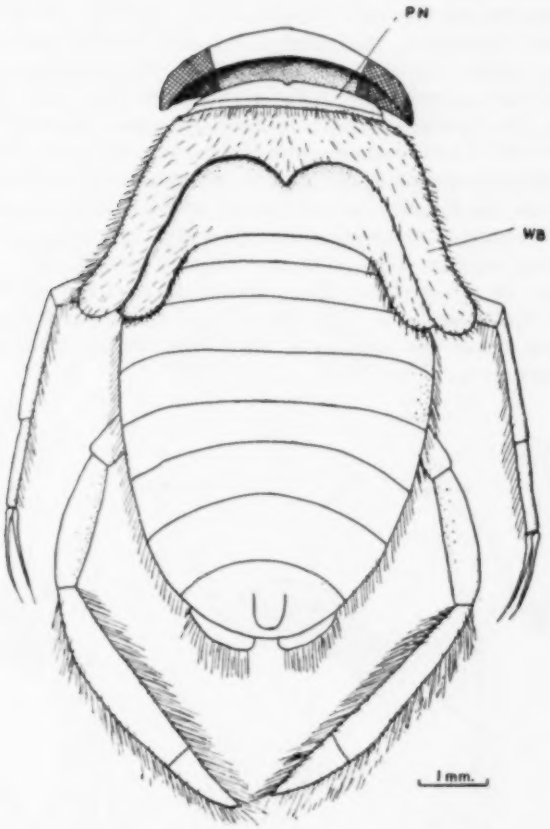

Fig. 11.—*Corixa punctata*. Dorsal view of fifth instar. PN Pronotum ; WB Wing buds.

Corixidae are to be found in abundance in almost every type of aquatic habitat and are also some of the first to colonise temporary habitats. This family of insects shows a greater degree of adaptation to aquatic life than most other groups of insects, yet retain its powers of flight. The combination of these features has made the Corixidae ecologically one of the most important families of fresh-water organisms.

DISCUSSION

Introduction

Brown's (1948) observations that the smaller instars of littoral Saldidae are able to withstand submergence, shows that immature stages of a terrestrial insect can invade water and live as aquatic organisms—respiration being cutaneous. There is a striking parallel between these early Saldid instars

and those of Ephemeroptera, Odonata, Plecoptera, Neuroptera and Trichoptera, but such an aquatic life presents two difficulties. Firstly, there is a gradual reduction in the respiratory efficiency of the skin, as the insects grow, and secondly, there is the difficulty of changing to the tracheal respiration of the adult. In most aquatic insects, these two difficulties are solved independently. Thus, the ephemeropteran nymphs use the abdominal 'gills' to drive a respiratory water current over the body. In some Trichoptera, a respiratory current is produced by abdominal undulations within the larval case, while others, like the Plecoptera, live in running water. In many 'larval' Odonata and Neuroptera, the body surface is secondarily increased by tracheal gills, while many aquatic Coleoptera and Diptera periodically ventilate the tracheal system at the surface. These insects acquire the adult method of respiration at metamorphosis. The presence of a terrestrial pupa in aquatic Coleoptera means that the larval and adult adaptations to aquatic life are mutually independent.

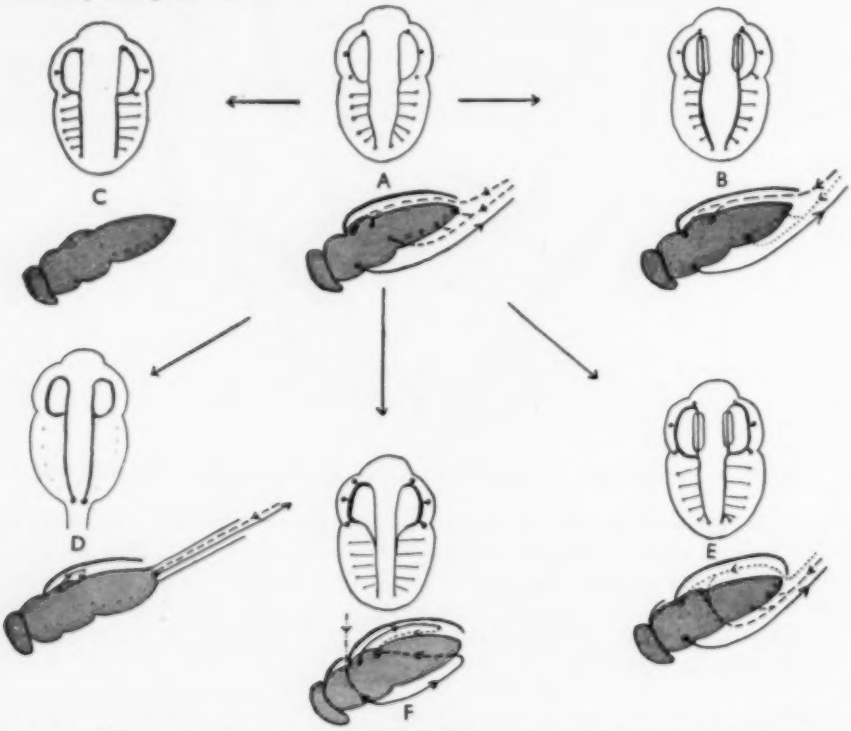

Fig. 12.—The tracheal systems are respiratory air currents of aquatic Hemiptera Heteroptera. — — — — — — —Main inspiration air current ;.....Subsidiary inspiration air current ; ————————Expiration air current ; —·—·—·—·— Gas store replenishment air current (*Corixa*). A. Hypothetical ancestral type ; B Naucorid type (*Ilyocoris cimicoides*) ; C Aphelocheirid type (*Aphelocheirus aestivalis*) ; D Nepid type (*Nepa cinerea*) ; E Notonectid type (*Notonecta glauca*) ; F Corixid type (*Corixa punctata*).

From these aquatic insects the Hemiptera stand apart, in as much as the growing nymphs compensate the reduction in the respiratory efficiency of the skin by using the physical gill, thus acquiring simultaneously the adult method of respiration and the whole life cycle becomes aquatic. The range of respiration methods amongst the Hemiptera Heteroptera can be explained with reference to a series of major types, no evolutionary significance necessarily being implied.

If the primitive Ochteridae, Gelastrocoridae, Helotrephidae and Saldidae show a level of organisation similar to that of ancestral water bugs, it seems reasonable to suggest that aquatic Hemiptera Heteroptera have evolved

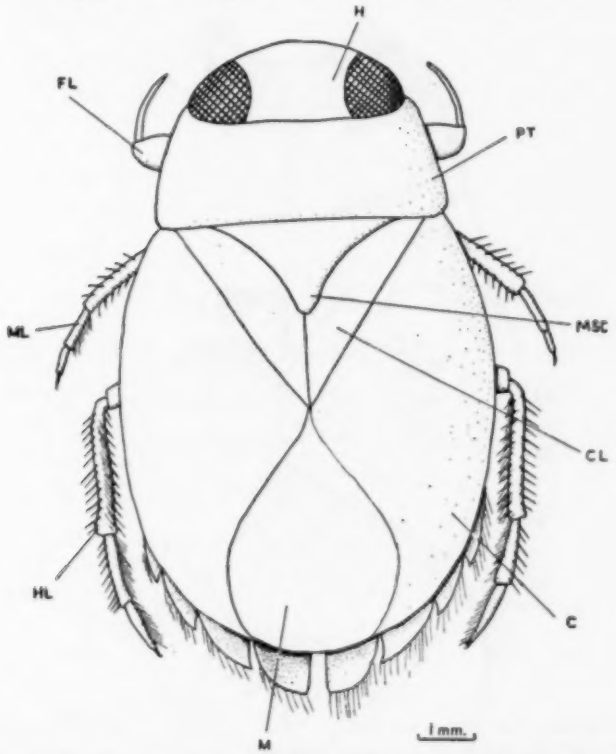

Fig. 13.—*Ilyocoris cimicoides*. Dorsal view. C Corium ; CL Clavus ; FL Front legs ; H Head ; HL Hind legs ; M Membrane ; ML Middle legs ; MSC Mesoscutellum ; PT Prothorax.

from a small predaceous, non-flattened winged bug with an anatomy and morphology, in general, similar to *Corixa punctata* (described above), but with longitudinal thoracic and abdominal tracheal trunks equally well developed and the three pairs of legs unspecialised. It is also reasonable to suppose, this generalized water bug lived near the edge of aquatic habitats, that the early nymphal instars respired cutaneously, and later instars used air trapped between hairs, on the ventral abdominal surface, as a physical gill. Also a

comparison of the respiration of aquatic Hemiptera would seem to indicate air was inspired through the ventral abdominal and anterior abdominal spiracles, expiration occuring mainly through the anterior thoracic spiracles (Fig. 12A).

Naucorid type (as illustrated by *Ilyocoris cimicoides* Stål) closely approximates to this generalized type, but differs from it in having the body dorsoventrally flattened (Figs. 12B, 13 and 14) and in having a pair of median (Fig. 15 MAT) and two pairs of lateral thoracic air sacs (Fig. 15 TA), doubtless adaptations to large body size. *Ilyocoris cimicoides* is predaceous amongst marginal aquatic vegetation, prey being captured between the tibiae and tarsi of the front legs (Figs. 13 and 14).

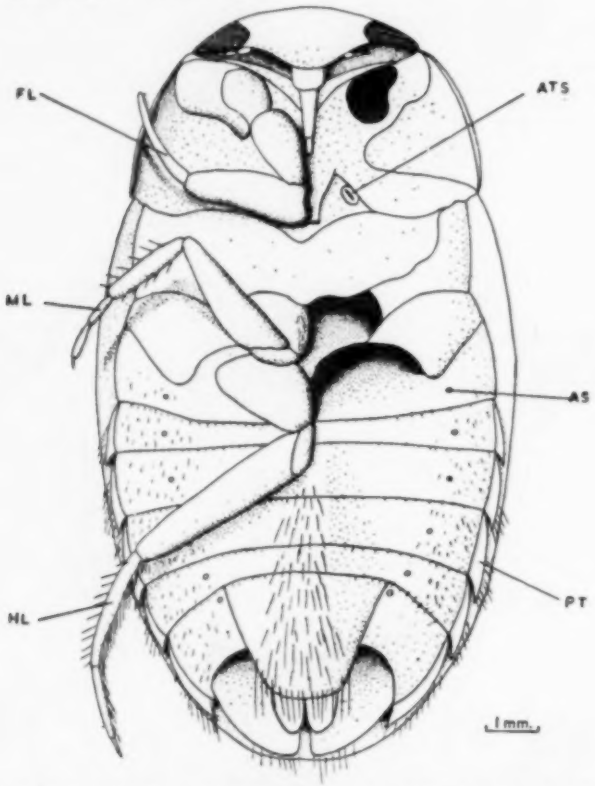

Fig. 14.—*Ilyocoris cimicoides*. Ventral view. AS Anterior abdominal spiracles ; ATS Anterior thoracic spiracles ; FL Front legs ; HL Hind legs ; ML Middle legs ; PT Paratergites.

Ilyocoris surfaces for several minutes, floating at the surface with the head inclined downwards at an angle of 30 degrees. In this position, the genital segments are extruded, and expose a dorsal depression on the 8th and 9th abdominal segments (Fig. 16B), which is continuous with the sub-hemielytral air store. One each side, a depression near the edge of the ventral surface of the hemielytra (Fig. 16A, D) fits on a dorsally directed peg-like structure

(Fig. 16a, P) of the pleura at the meso- metathoracic junction. In this way the hemielytra are held firmly in place. The sub-hemielytra air space is enlarged by depression of the abdomen and the main inspiration air current (Fig. 12B) passes forwards under the wings into the anterior abdominal and posterior thoracic spiracles—the lateral groove and ridge being less developed than in *Corixa*. Sometimes the insects surface in a more vertical position and occasionally float with the ventral surface uppermost as in *Notonecta*. A subsidiary air current (Fig. 12B) is then inspired through the posterior abdominal spiracles. The ventral gas store is held in position by hydrofuge hairs on the

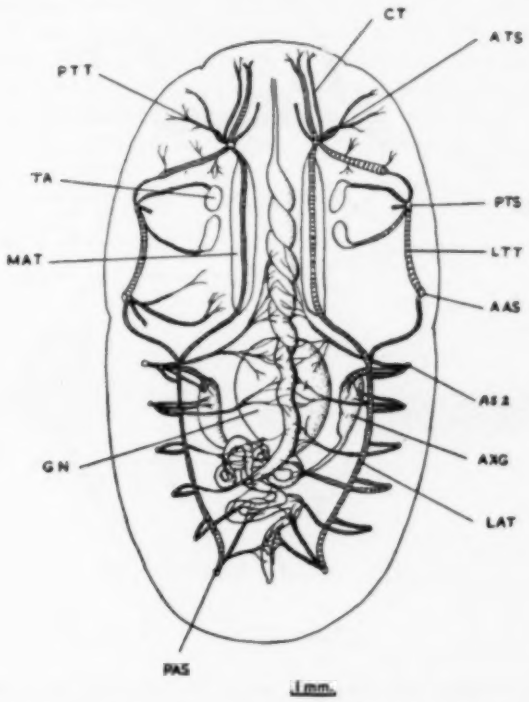

Fig. 15.—*Ilyocoris cimicoides*. Tracheal system. ASS Anterior abdominal spiracle ; AS 2 Second abdominal spiracle ; ATS Anterior thoracic spiracle ; AXG Auxiliary gland ; CT Cephalic tracheae ; GN Gonad ; LAT Longitudinal abdominal tracheal trunk ; LTT Longitudinal thoracic tracheal trunk ; MAT Median thoracic air sac ; PAS Posterior abdominal spiracle; PTS Posterior thoracic spiracle ; PTT Prothoracic tracheae ; TA Lateral thoracic air sac.

ventral abdominal surface. Air is mainly expired through the anterior thoracic spiracles and is then moved backwards over the ventral thoracic surface by the femora of the hind legs and over the ventral surface of the abdomen by the tibiae and tarsi of the same appendages. At temperatures of 20°C or more a large gas bubble gradually accumulates at the posterior end of the ventral body surface and is released when the insects rise to replenish the gas stores. Unlike the

action of *Corixa*, the hind legs are not rubbed over the wings and this suggests air is not expired from the dorsal spiracles. During submergence, the ventral gas stores are normally thin but tend to shrink and become less widely distributed owing to the solution of carbon dioxide and nitrogen.

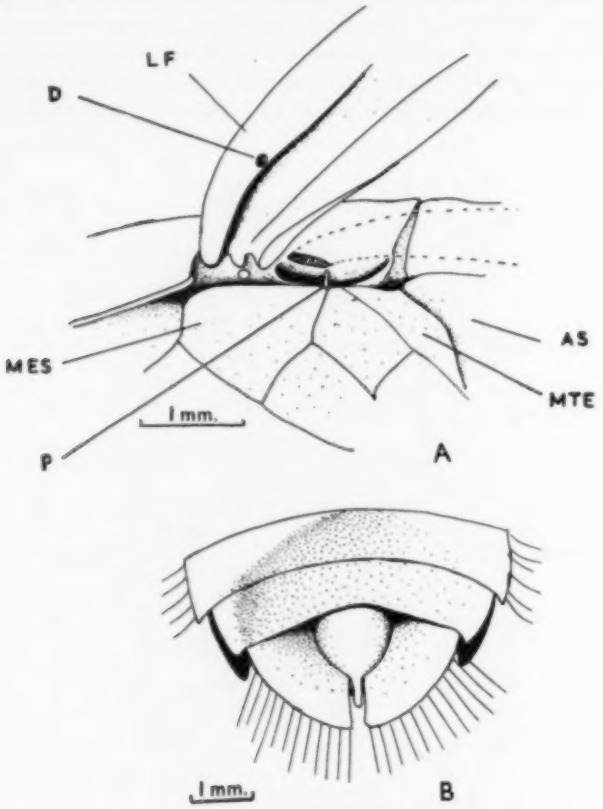

Fig. 16.—*Ilyocoris cimicoides*. A. Lateral view of the thorax to show the lateral groove. AS First abdominal sternite ; D Depression on the underside of the hemielytron ; LF Lateral flange of reflexed hemi-elytron ; MES Mesepimeron ; MTE Meta-episternum ; P Peg like process.
B. Dorsal view of posterior abdominal segments to show dorsal depression.

The superficial gas stores of aquatic Hemiptera can be replenished by surfacing in stagnant or slowly moving water, but not in fast flowing streams or rivers, where the water is turbulent by flowing over a stony bottom. Yet, on account of the high tension of dissolved oxygen present, such a habitat is favourable to insects using a physical gill. An *aphelocheirid type* (Fig. 12C) (as exemplified by *Aphelocheirus aestivalis* Westwood) occurs in such conditions. The aphelocheirid type can be derived from the primitive type (Fig. 12A) by the formation of a plastron : gaseous exchange taking place through all spiracles.

Once a plastron had been acquired the need for gas store replenishment and for the hemielytra to collect air from the surface (as in the naucorid type) no longer existed. The loss of wings, flight muscles and the reduction of the median thoracic tracheal trunks can be explained as adaptations to permanent submergence in this specialized type of habitat.

Nepid type (Fig. 12 D) (as exemplified by *Nepa cinerea* L. and *Ranatra linearis* L.) resembles the naucorid type in the raptorial form of the front legs, which are of little value in swimming. These insects are also predators in marginal aquatic vegetation, but their methods of respiration show evolutionary trends independent of the remainder of the Cryptocerata. On the ventral body surface, nymphs of *Nepa* carry a gas store into which the spiracles open. This gas store could function as a physical gill, but gaseous exchange mainly takes place through the cavity of the respiratory tube and the posterior abdominal spiracles. As the nymphs grow they depend more and more upon surface tracheal ventilation through the caudal filaments. According to Hamilton (1931) the longitudinal abdominal tracheae of the adult are well

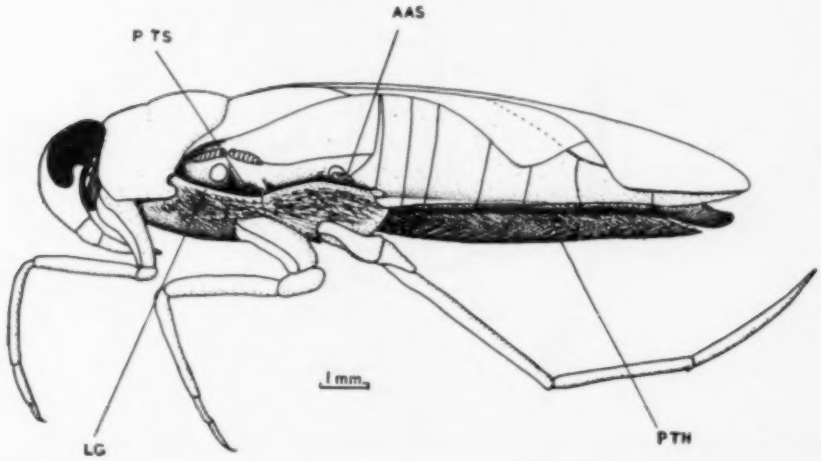

Fig. 17.—*Notonecta glauca*. Lateral view (Left wings removed). AAS Anterior abdominal spiracle ; LG Lateral groove ; PTS Posterior thoracic spiracle ; PTH Hairs of paratergite.

developed, but the anterior thoracic and anterior abdominal spiracles are reduced, while the remainder of the abdominal spiracles are closed. The work of Brocher (1916) has shown the functional posterior thoracic spiracles are used for gaseous exchange between the tracheae and the sub-hemielytral gas store—the air being derived not from the atmosphere but the tracheae. The closure of the abdominal spiracles is associated with loss of the ventral gas stores and physical gill respiration. The subsidiary air stream through the posterior abdominal spiracles of the naucorid type has, in *Nepa*, become greatly developed, and these spiracles are also used for expiration. In the Belostomatidae, gaseous exchange occurs both through the sub-hemielytral gas store and the

posterior abdominal spiracles at the base of the respiratory tube and thus shows a condition intermediate between the naucorid and nepid types in this respect.

Notonectid type (as exemplified by *Notonecta glauca* Figs. 12E, 17, 18 and 19) shows another evolutionary trend. *Ilyocoris cimicoides* occasionally surfaces with the ventral side uppermost and catches insects with its front legs at the air-water interface. This behaviour is of special interest, because it shows

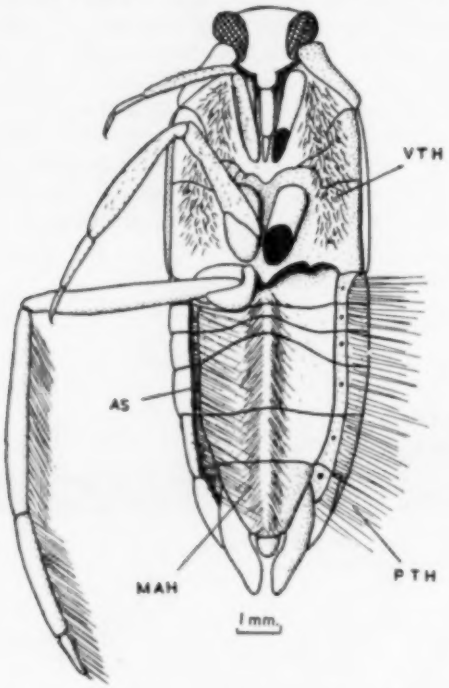

Fig. 18.—*Notonecta glauca*. Ventral view. AS Abdominal spiracle ; MAH Median row of abdominal hairs ; PTH Hairs on paratergites ; VTH Ventral thoracic hairs.

how the notonectid type might have evolved from the generalized type described above. At the water surface many aquatic larvae undergo metamorphosis, others go there to replenish their gas stores or ventilate their tracheal system, while not a few adults visit the surface for oviposition or drinking. Many drowned terrestrial animals are to be found floating in the surface films. This rich source of food supply is available to any aquatic bug, which can float inverted under the surface and hold its food in the anterior legs. It is this niche which the notonectid type has occupied.

The notonectid type (Fig, 12E) can be derived from the generalized type, by turning the insect ventral side uppermost and making the first and second pairs of legs raptorial for prey capture. If the sub-hemielytral air store is greatly enlarged, the insect will float with the tip of the abdomen touching the

air-water interface, the head pointing obliquely downwards. In *Notonecta glauca*, the hemielytra lie at an angle to the dorsal body surface, meeting in the mid dorsal line to form a small keel. The membrane of the right hemielytron overlaps that of the left and the two wings are thus held firmly together, enclosing a posterior air space. In addition, the abdominal spiracles, on each side, lie between two rows of longitudinal rows of hydrofuge setae and the ventral

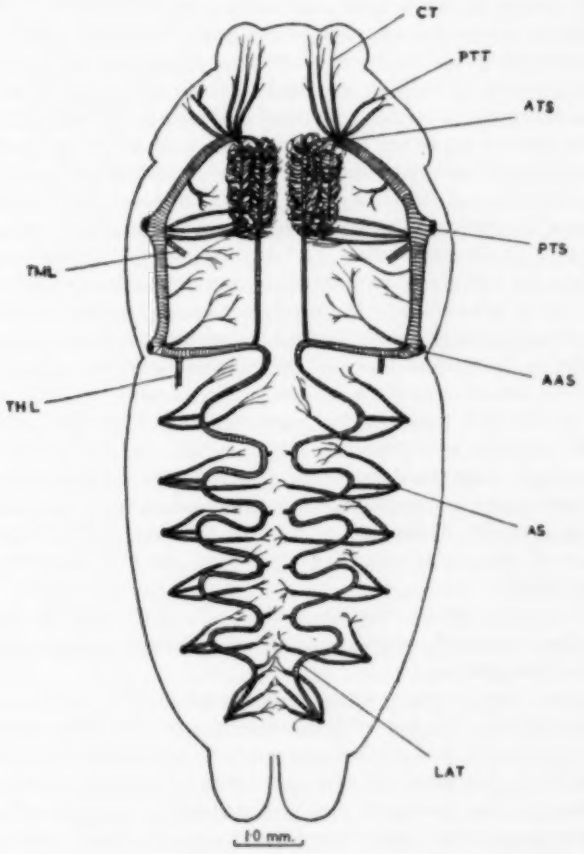

Fig. 19.—*Notonecta glauca*. Tracheal system. AAS Anterior abdominal spiracles ; AS Third abdominal spiracles ; ATS Anterior thoracic spiracles ; CT Cephalic tracheae ; LAT Longitudinal abdominal tracheal trunk ; PTS Posterior thoracic spiracles ; PTT Prothoracic tracheae ; THL Trachea to hind leg ; TML Trachea to middle leg.

surface of the thorax bears long setae, which restrict the surface gas stores to the mid ventral line (Fig. 18). Compared with the naucorid type, *Notonecta glauca* only occasionally inspires through the sub-hemielytral gas store, and the main inspiration current takes place through the ventral gas store into which

the abdominal spiracles open. The posterior edge of the meta-episternum lies in a groove on the anterior margin of the sternite of the second abdominal segment and encloses a lateral channel which connects the ventral gas stores with the dorso-laterally placed anterior abdominal spiracles. The tracheal system (Fig. 19), in general, resembles that of *Corixa*, except that the longitudinal tracheal trunks of the abdomen are better developed, though to a lesser extent than in *Ilyocoris*, and shows a condition intermediate between *Ilyocoris* and *Corixa* in this respect. If the posterior abdominal spiracles were the main centres for inspiration, as in *Nepa*, one would expect the longitudinal abdominal tracheal trunks to be well developed, but the fact the trunks are somewhat reduced suggests that gaseous intake occurs mainly through the anterior abdominal spiracles: the longitudinal abdominal tracheae, unlike *Corixa*, allowing some gaseous exchange to take place between the thorax and abdomen.

Expiration mainly occurs through the anterior abdominal spiracles. When this occurs the centre of buoyancy moves forwards and the insects float in a more horizontal position. The front and middle legs (Figs. 17 and 18) bear large numbers of hydrofuge setae, and by means of " cycling movements " these legs move the bubbles of expired air backwards medially along the ventral body surface to be released into the water or the atmosphere. As the ventral abdominal surface comes close to the air-water interface, the hydrofuge hairs become caught in the surface film and are rotated upwards and outwards, thus exposing the ventral abdominal spiracles. Occasionally, expired air is passed by the tips of the hind legs into the posterior end of the sub-hemielytral gas store. If the pressure is slightly increased, bubbles of gas, which could only have been expired from the dorsal spiracles, appear lateral to the hind coxae.

These observations on the functions of the various spiracles largely confirm those of Hoppe (1912) rather than those of Brocher (1909), who suggested the hind pair of abdominal spiracles were used only for inspiration and the others for expiration.

The work of Ege (1915), Thorpe & Crisp (1947-49) and De Ruiter *et alii*. (1952) have also shown the surface gas stores function as a physical gill when the insect is submerged.

At low pond temperatures small insects can obtain sufficient oxygen by means of the physical gill, but with increase of size, the body surface becomes proportionately smaller and the efficiency of the physical gill reduced. When aquatic Hemiptera Heteroptera first submerge, they draw upon the oxygen initially present in the gas stores and then change to physical gill respiration. The larger the insects the more they depend upon tracheal ventilation at the water surface for their main oxygen supply. The Nepidae, Belostomatidae, Naucoridae and Notonectidae comprise some of the largest of water bugs, which are precluded by their methods of respiration from venturing far from the surface or remaining submerged for prolonged periods. Compared with the remainder of the Cryptocerata the Corixidae stand apart. These small water bugs depend upon the physical gill for their main oxygen supply and their ability to remain submerged for long periods has enabled them to become adapted to bottom habitats and to which they have undergone adaptive radiation evolving into more than 100 Palearctic species.

The Corixid type (as exemplified by *Corixa punctata*) (Fig. 12 F), differs from the generalized type in that the longitudinal abdominal tracheal trunks are greatly reduced, compared with those of the thorax, and the anterior abdominal spiracles are the main inspiration centres : the main gas stream entering from the ventral surface under the mesad to the meta-episternum, while a subsidiary air stream is derived from the sub-hemielytral gas store. Gas expired from the anterior thoracic spiracles passes backwards over the ventral body surface, for gaseous exchange with the dissolved gases in the surrounding water, while a subsidiary current of expired air from the posterior thoracic spiracles is passed backwards, by the hind legs, to the sub-hemielytral gas store. By circulating gas over the body surface and through the thorax in this way, the efficiency of the physical gill is greatly increased and the thoracic muscles of locomotion receive a continuous oxygen supply. Unlike the process in other types of aquatic Hemiptera, gas replenishment takes place anteriorly by momentary contact of the pronotum and wing bases with the air-water interface. The respiration and tracheal system of *Micronecta poweri*, in general, resemble that of *Corixa punctata*, but the longitudinal trunks of the abdomen are relatively better developed. In this respect *Micronecta* shows a condition intermediate between *Ilyocoris* and *Corixa*.

The relationship between the main types of aquatic Hemiptera Heteroptera is illustrated by Figure 12.

Secondary features

Surfacing

The use of the physical gill is not devoid of difficulties. In the first place, insects have little difficulty in remaining permanently submerged, when the tracheal system is closed and cutaneous respiration affords an adequate oxygen supply. Insects using a physical gill must surface as soon as the gas stores shrink to a critical stage and an oxygen debt is incurred. This problem seems to have been solved in various ways amongst the Hemiptera. *Aepophilus bonnairei* Sign. remains inactive during submergence, thereby reducing oxygen consumption to a minimum (Leston 1956). Salt marsh Saldidae behave in a similar manner (Brown loc. cit.). This method can be used by littoral insects, which will be exposed within a few hours at the next low tide, but it cannot be used by active bottom living insects, such as corixids, in non-tidal waters. For this reason, the evolutionary potentialities of this method are limited. Most aquatic Hemiptera and Coleoptera insects need some mechanism to bring them to the surface as soon as an oxygen debt begins to be incurred. Without such a surfacing mechanism the course of the evolution of these aquatic insects would be prematurely terminated. Moreover, this surfacing mechanism must be present *before* the insects invade water for the first time in their evolutionary history, and will also indirectly prevent the insects from wandering to a depth where the tracheal system might be flooded.

So far as corixids are concerned there would appear to be two such mechanisms. The first is provided by the buoyancy of the gas stores themselves, which automatically lift the insect to the surface when it relinquishes its hold of the bottom, and the second is provided by the phototactic reactions

described above. There is ample evidence that flying insects have a high oxygen deficiency, and the popular method of collecting flying insects in light traps is good evidence these insects are also positively phototactic. The association between positive phototaxis and oxygen deficiency would seem to be widespread amongst insects. When, therefore, submerged insects develop an oxygen debt due to depletion of the gas stores, they will tend to become positively phototactic and are guided by light to the air-water interface.

Pressure perceptors

Should aquatic Hemiptera wander to too great a depth, there is a danger of the gas stores shrinking and water flooding the tracheal system. Thorpe & Crisp (loc. cit.) have demonstrated the existence of special pressure perceptors associated with the abdominal spiracles of *Aphelocheirus* and Baunacke (1912) has described similar organs in the nymphs of *Nepa*. In both these insects abdominal gaseous exchange is not accompanied by gas movements of the magnitude such as occur in *Corixa* or *Notonecta*. Wefelscheid (1912) has described in *Plea* a small membrane separating the lateral tracheal thoracic trunks from the exterior, situated on the inner wall of the lateral thoracic pouch. The centre of the membrane bears a lump to which are attached scolophore cells. A similar organ exists in *Ilyocoris* and *Notonecta*. Though Wefelscheid (loc. cit.) suggested the organ in *Plea* had an auditory function, it might also perceive pressure changes. The greater complexity of Hagemann's organ in *Corixa* (described above) is doubtless associated with the greater depth to which these insects descend.

Locomotion

Aphelocheirus crawls upon the habitat bottom and *Nepa* does the same amongst pond weed. In these insects, the middle and hind legs are relatively unspecialized, and the insects can only swim with difficulty. In *Ilyocoris* the gas stores are relatively thin and the density of the insect approximates to that of water. This insect swims amongst weed by means of the middle and hind legs, which are slightly flattened and fringed with hairs which increase the functional leg surface. The inverted position of *Notonecta* is associated with an elongation of the hind legs for swimming. In *Corixa*, bottom feeding is associated with the specialized form of the front legs, while the middle legs are needed to anchor the insect to the substratum. The hind legs are long, flattened and fringed with hairs and used for swimming. Both *Corixa* and *Notonecta* carry so much air on the body surface that, with their gas stores, they are appreciably lighter than water and tend to float towards the surface between each leg kick. To compensate for this the hind legs must not only drive the insects forward but also slightly downwards. Associated with this the hind coxae are rotated backwards and inwards and the leg kick is not only backwards but also slightly upwards (Popham 1952).

Mating habits

In *Nepa*, *Ilyocoris* and *Notonecta* gas store replenishment occurs at the posterior end of the insect. When these insects mate, the male grips the female round the prothorax with his front legs, while the genitalia are extruded and twisted until the aedeagus is inserted into the vulva of the female. While

joined in this way the pair can surface and replenish their gas stores in the normal way. In *Corixa*, gas store replenishment takes place anteriorly, air entering the gas stores between the pronotum and pterothorax. While the pair are copulating, gas store replenishment cannot take place in the normal way. This is associated with specialized mating habits which may be summarized as follows.

The male first makes a sudden dart on to the back of the female, which he grasps on either side of the prothorax with his short front legs. The male flattens himself on the female and his facial depression fits over the convex dorsal surface of the female pronotum. The male abdomen is asymmetrical, the genitalia being on the left side in *Corixa punctata* and related species. The male abdomen has a deep lateral V shaped invagination between the fifth and sixth abdominal segments on the side of the asymmetry (See Macan 1956 p. 37). The aedeagus is capable of great extension and when protruded curls upwards and forwards over the back of the abdomen through the lateral gap between the fifth and sixth segments into the posteriorly placed female vulva. The two insects are firmly held together, both anteriorly and posteriorly. When joined in this way, the two sexes have difficulty in renewing their gas stores, because the male is flattened against the dorsal surface of the female and is, therefore, unable to bend his head and prothorax, while the female, being ventral to the male is unable to contract the surface in the normal way. When surfacing, the pair roll over on to the side of the male asymmetry and gas uptake occurs on the other side of the body. The asymmetry of the male abdomen allows the two insects to remain attached on one side, while the other is given a greater degree of freedom of movement for gas store replenishment.

CONCLUSIONS

The tracheal systems and methods of respiration of the main types of Hemiptera Heteroptera, described above, are so different that each would seem to represent a separate evolutionary trend from a common ancestral type, in many respects perhaps not unlike that of *Ilyocoris*. The belostomatid type would appear to be intermediate between the naucorid and nepid types, the notonectid type showing quite independent evolutionary trends. These deductions agree with the phylogeneric relationships as described by China (1933), who regarded the Helotrephidae as showing a primitive level of organisation from which could be derived on the one hand the Naucoridae, Belostomatidae and Nepidae and on the other the Pleidae and Notonectidae. The corixid type, however, presents special problems. The corixid method of respiration and form of the tracheal system could, in part, be derived from the notonectid type ; but the specialized function of the sub-hemielytral gas store, in making the insect very buoyant and in enabling it to float under the water surface with the body inclined obliquely downwards, must be regarded as an essential feature of the notonectid type and as an adaptation to surface predation. The evolutionary trends of the Pleidae and Notonectidae are, therefore, quite independent of those of the Corixidae, which are essentially bottom living animals, similarities between the two types being due to evolutionary convergence. In both insect types, there is a tendency for gaseous exchange to be concentrated

in the thorax and is, in each, associated with specialized swimming habits. One is, therefore, obliged to regard the corixid type as representing yet another independent evolutionary trend from a common ancestral type : a view which in confirmed by a comparison of the form and function of the front and middle legs of the notonectid and corixid types.

It has been assumed the common ancestor of aquatic Hemiptera Heteroptera was itself aquatic, and that the Cryptocerata is a natural group of animals ; but the evolutionary trends of the main types, described above, are so different that it would also not be unreasonable to suggest that the ancestral type was not aquatic, but terrestrial. In this case the Cryptocerata might well prove to be polyphyletic. This, however, is a matter for further investigation.

SUMMARY

1. The gas stores carried on the body surface of *Corixa punctata* (Illig.) function as " physical gill ".

2. The thoracic tracheal system is well developed and is largely independent of that of the abdomen. The abdominal longitudinal tracheal trunks are vestigial and the abdominal tracheal system has a primitive level of organisation.

3. Gas is expired through the anterior thoracic spiracles, moved backwards over the body surface by the hind limbs and inspired through the anterior abdominal spiracles. The arrangement of the thoracic sclerites and meta-thoracic leg muscles suggests the thoracic tracheal system is automatically ventilated during swimming.

4. Corixids surface from abnormal depths owing to the stimulation of Hagemann's organ, but normally owing to deficiency of oxygen.

5. The process of surfacing is described and the function of the rastration of the pronotum and corium discussed.

6. Corixids are positively phototactic when deficient of oxygen but normally negatively phototactic.

7. Cutaneous respiration in the first instar is gradually replaced by a greater use of the surface gas stores as physical gills. It is suggested this is a way of compensating for the reduction in the relative size of the body surface, the increased thickness of the cuticle in later instars ; these changes reducing the efficiency of the body surface as a respiratory organ.

8. The use of the surface gas stores as a physical gill makes the insect lighter than water. The hind legs, therefore, have to drive the insect towards the bottom when progressing along a horizontal path. This is associated with a forward slant of the thoracic segments and a backward and median rotation of the hind coxae.

9. It is suggested that the asymmetrical male abdomen allows male and female in cop to be held together on one side of the body, while gas store replenishment takes place on the other.

10. The methods of respiration of various members of the Hemiptera Heteroptera are discussed and summarized in Fig. 12.

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THE DEVELOPMENT OF THE LAMELLIBRANCH *CARDIUM EDULE* L.

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(With 6 figures in the text)

The development of *Cardium edule* is described from the fertilization of the eggs to the completion of metamorphosis. Cleavage and gastrulation are similar to those processes in other lamellibranchs. Differentiation of the major larval organs, the velum, the larval retractor muscles and the digestive system is completed within the first four days of life. Other organs are relatively undeveloped until the veliger is twenty-two to twenty-five days old. Differentiation is not complete until the spat have settled for several weeks. The larval retractor muscles are paired and are attached around the mouth and to the presumptive foot region as well as to the velum.

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INTRODUCTION

Lovén (1848) gave drawings and a brief description of the different stages in the development of *Cardium edule* one of the first lamellibranch larvae to be reared and described. Since that time the embryology of other molluscs has been intensively studied and a further investigation of *Cardium* seems desirable.

The most detailed researches into lamellibranch embryology are those made over fifty years ago by Lillie (1895) on the Unionidae and Meisenheimer (1901) on *Dreissensia polymorpha*. All the species described live in freshwater so one might expect them to differ in detail from the marine species. The major descriptions of development of common marine forms are those of *Pholas* (Sigerfoos, 1895), *Nucula* and *Yoldia* (Drew, 1899, 1901), *Ostrea virginica* (Stafford, 1913) *Mytilis edulis* (Field, 1922) and *Hiatella orientalis* (Miyazaki,

1938b). Of these *Nucula* and *Yoldia* develop atypically and in the other species descriptions of cleavage and the early stages are based on living specimens and whole mounts.

Interest in lamellibranch larvae has increased lately because they constitute an important element in the plankton of inshore waters. Lebour (1938) reared to metamorphosis and described the external features of species of numerous genera including two of *Cardium*, Jørgensen (1946) described the external features of many veliger larvae and Quayle (1952) give a detailed account of the late veliger and spat of *Venerupis* (=*Paphia*) *pullastra*.

METHODS

Adult specimens of *Cardium edule* L. were collected from the estuary of the River Dovey at intervals of about four weeks throughout the year and their gonads were examined and sectioned. Specimens with mature gonads were found from February until the last week in May, when spawning takes place if the weather is normal. During the cool spring and summer of 1954 it was delayed by about ten days.

Stages in the development of the cockle were obtained by rearing artificially fertilized ova in plunger jars. This was most successful at or near the breeding season. Earlier it was difficult to find ripe females—specimens from which rounded ova streamed into the water as soon as the gonadial wall was broken. The condition of the males seemed less important, possibly because all mature males contain some ripe and active sperm.

Larvae were reared in filtered sea-water in plunger jars until they were twenty-five days old. After the third day it was important to feed the veligers adequately and to correct the salinity of the culture if there was much evaporation. The food was taken from a culture of Flagellate I (*Isochrysis galbana*) reared according to the method of Bruce, Knight & Parkes (1940) : veligers from the surface water and newly metamorphosed animals from the cockle beds were also examined.

Narcotisation was essential for an examination of all but the earliest stages ; the most successful way of achieving it was to add drops of 5 per cent urethane (in sea water) very slowly to a petri dish of larvae.

SEASONAL CHANGES IN THE GONADS

Johnstone (1899) described the anatomy of the genital system in spring immediately before spawning. The main ducts, lateral ducts and alveoli he described were traced easily in specimens collected between January and June. At this time of the year each gonad opens to the exterior by a short terminal ciliated duct into which open a small number of collecting ducts. These collecting ducts branch repeatedly, the ultimate blind branches being the alveoli. The walls of all except the latter have a narrow ciliated strip along their length the rest of the wall being germinal epithelium. In their fully developed condition the gonads form a considerable portion of the contents of the visceral mass ; although diffuse structures they are mainly peripheral to the digestive system (including the digestive gland lobes) and lie immediately below the outer muscular covering of the visceral mass. After the breeding season is

over only the largest ducts are distinguishable and the short terminal duct behind the genital opening contains mucus mixed with degenerating ova or sperm.

By October a few primary sex cells have developed on the unciliated portion of the walls of the larger ducts but it is impossible to tell the sex of specimens until late November when oocytes are easily distinguished from the smaller deep-staining and radially arranged spermatocytes. Development continues slowly throughout the winter ; by January there are a few ripe ova and sperm in the main ducts and the lateral ducts and alveoli are visible again, packed with differentiating germ cells. Growth and differentiation are very rapid during the spring so that in April the posterior part of the visceral mass is greatly distended and by May most of the ova and sperm are ready to be shed.

DEVELOPMENT

Cleavage is rapid in *Cardium edule* so that at normal room temperatures (10-15°C.) gastrulation is complete about twenty-four hours after fertilization. The gastrulae soon develop cilia and after forty-eight hours well developed trochophores are rotating rapidly within their gelatinous envelopes. During the next two days the larger velar cells differentiate at the anterior end and the visceral mass enlarges and is covered by a recognizable lamellibranch shell. On the fourth day the retractor muscles are sufficiently developed for the larva to retire between its two shell valves if it is disturbed. At this stage laboratory reared specimens are about 112μ long.

Small metamorphosed specimens (shell valves 280 μ long) were collected from the cockle beds during the second week in June. Since the main spawning occurs at the end of May the veliger stage probably lasts two to three weeks. The tiny metamorphosed cockles had two or more ctenidial filaments and have lost the velum. They were very active and, as Baggerman (1953) suggests, did not settle for long in one position.

Cleavage.

The greyish white ova are about 50μ in diameter when they are shed and, as Lebour (1938) describes, are surrounded first by a thin membrane and then by a thick gelatinous covering 50 to 60 μ thick. Three hours after mixing ripe ova and sperm, some ova have given off polar bodies and others have progressed further and undergone the first cleavage. This is unequal ; one daughter cell is 35 μ and the other 28 μ across within their covering membranes (Fig. 1A.). The cells do not separate but are closely pressed to one another. The four cell stage is reached about six hours after fertilization. The smaller of the two blastomeres divides equally and the larger unequally, so that three small cells of approximately equal size and one large cell are formed (Fig. 1B.). In spite of the difference in size of the cells the next divisions take place almost simultaneously so that nine hours after fertilization there are eight cells (Fig. 1C.). Two of these (W and Z) are much larger than the others and are formed from the large cell of the previous stage. They are not of equal size however. Of the six remaining cells three are larger than the others.

After this, division occurs somewhat irregularly but when fifteen to twenty cells are present they still form three groups according to size :—a number of small cells at the former animal pole (Fig. 1D, mi.), fewer medium sized cells vegetal to them (ms), and two very large cells (W and Z). Of these two very conspicuous cells one is still larger than the other. At this stage the larva has a small blastocoele which increases in size when further division takes place but never becomes as large as in *Dreissensia* (Meisenheimer, 1901). By reason of their size the two large cells project into the blastocoele until twenty-five to thirty cells are present, when they divide. In this division and those sub-

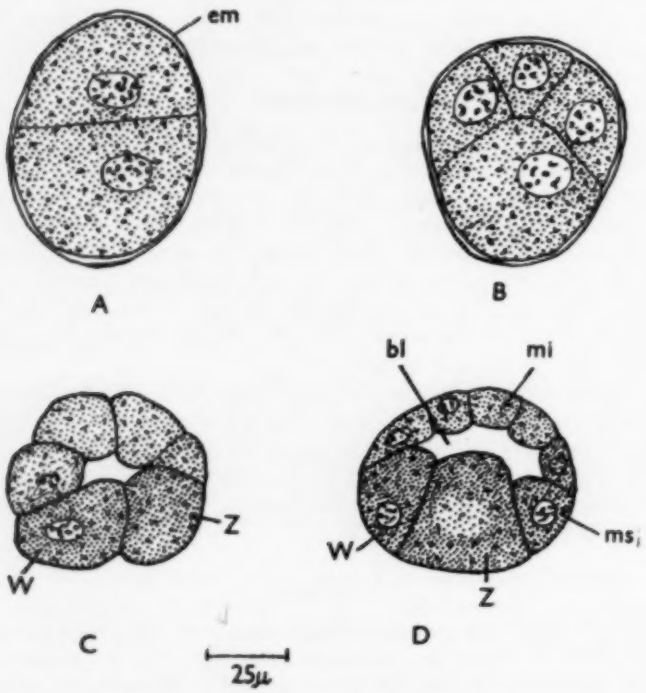

Fig. 1.—Cleavage in *Cardium edule* A. 2-cell stage ; B. 4-cell stage, C. L.S. 10-cell stage; D. bl, blastocoele ; em, egg membrane ; mi, micromeres ; ms, medium sized cell of 17 cell stage ; W.Z. very large macromeres.

sequent to it their daughter cells are of approximately equal size but larger than the other embryonic cells. The descendants of the largest cell, Z of the 8-30 cell stage, together with the previously described " medium " sized cells invaginate to form the digestive system ; the cells derived from the other large cell W lie near the future dorsal surface of the embryo and soon constitute a group of large cells from which the shell gland develops. The mesoderm is derived from a single cell lying between the presumptive shell gland and the vegetative pole. I have been unable to trace its origin. This cell sinks into the

blastocoele immediately before gastrulation. At first it is vase-shaped, the main body of the cell lying within the blastocoele connected to the surface by a narrower neck. The neck persists until gastrulation in complete and the mesoderm mother cell has divided (Fig. 2, me) to give one cell in contact with the surface and a second in the blastocoele.

Invagination is the most important process in gastrulation and it takes place very rapidly when the embryo is about twenty-three hours old. It is aided by

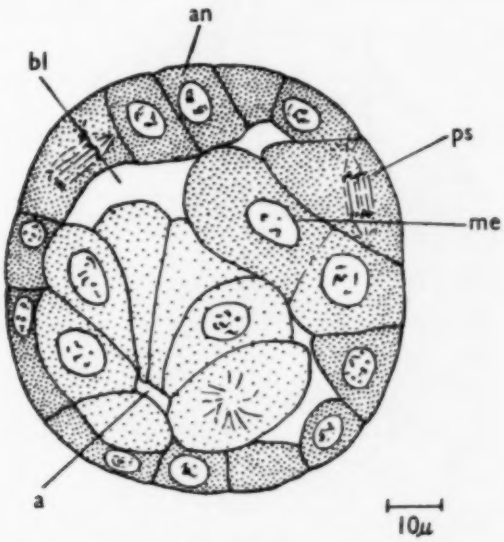

Fig. 2.—L.S. gastrula to show formation of the mesoderm. a, archenteron ; an, animal pole cells ; bl, blastocoele ; me, mesoderm ; ps, future shell gland.

the increase in small ectodermal cells which begins at this time. Externally the young gastrula is still a rounded mass about 60 μ in diameter (Fig. 2) but differentiation has already begun and its outer layer of cubical cells is not uniform. The cells at the animal pole which will form the velum and apical plate (an) and those on the future dorsal surface which will form the shell gland (ps) are slightly larger than the others. The gut is a rounded sac, and its narrow lumen is surrounded by large and elongated cells conspicuous because the cytoplasm stains less densely than in other parts of the embryo. The invaginated cells almost fill the blastocoele and press the mesoderm towards the developing apical plate. At gastrulation *Cardium* embryos are not ciliated but after a few hours the anterior surface is covered with fine short cilia and these cause slow rotation within the gelatinous envelope, which persists until the early veliger stage.

Rapid division of all the cells follows gastrulation so the blastocoele is soon obliterated and the lumen of the gut becomes very narrow. The blastopore narrows but continuity between the gut walls and the epidermis around the site of the blastopore in the region where the stomodaeum will invaginate

remains. By forty hours the trochophore is a solid ball of differentiating cells. Within it the gut has grown into a U-shape, the mouth and anus are on the ventral surface not far from one another, and the digestive gland rudiment is represented by a few large cylindrical cells at the curve of the U.

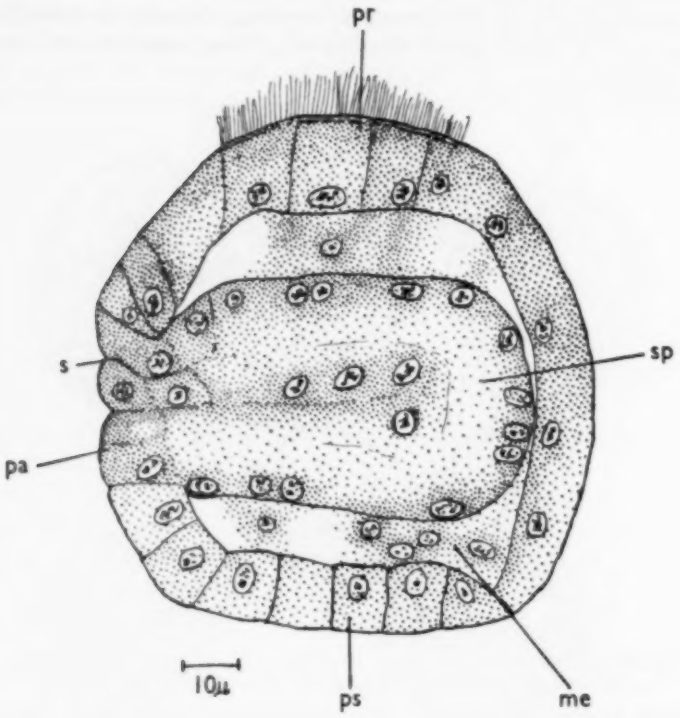

Fig. 3.—Sagittal section of 48 hour trochophore. me, mesoderm ; pa, future anus ; pr, prototroch; ps, future shell gland ; s, stomodaeum ; sp, future stomach.

Lateral to the gut are collections of small mesodermal cells. These are so closely packed between the gut wall and the outer layer that it is impossible to see whether they form two mesodermal bands such as those described in *Ostrea* by Fernando (1931). On the anterior surface the ciliated prototrochal cells are relatively large in size and vacuolated basally. The point of closure of the blastopore lies postero-ventral to this ciliated mass and moves rapidly closer to it with the growth of the shell gland. Postero-dorsally the presumptive shell gland is still represented by a single patch of relatively large cells. Within a few hours however they divide rapidly and for a time may form a slight depression in the surface. This is never a deep invagination such as is described by Meisenheimer (1901) in *Dreissensia*. As a result of rapid growth the shell gland covers the dorsal surface of the two and a half day larva. While the shell gland is growing the epidermal cells between it and the developing

velum and the velar cells themselves also divide and grow rapidly. The accelerated growth of these peripheral cells increases the volume of the larva considerably and spaces again appear around the gut and in the mesoderm.

At forty-eight hours *Cardium* larvae are typical trochophores (Fig. 3) but after three days development they are in the early veliger stage. Many other young lamellibranch larvae are similar ; the common features are the paired D-shaped shell valves, the prototroch (=velum) with its enlarged cells, the thickened apical region bearing a tuft of very conspicuous cilia, and the simple internal structure.

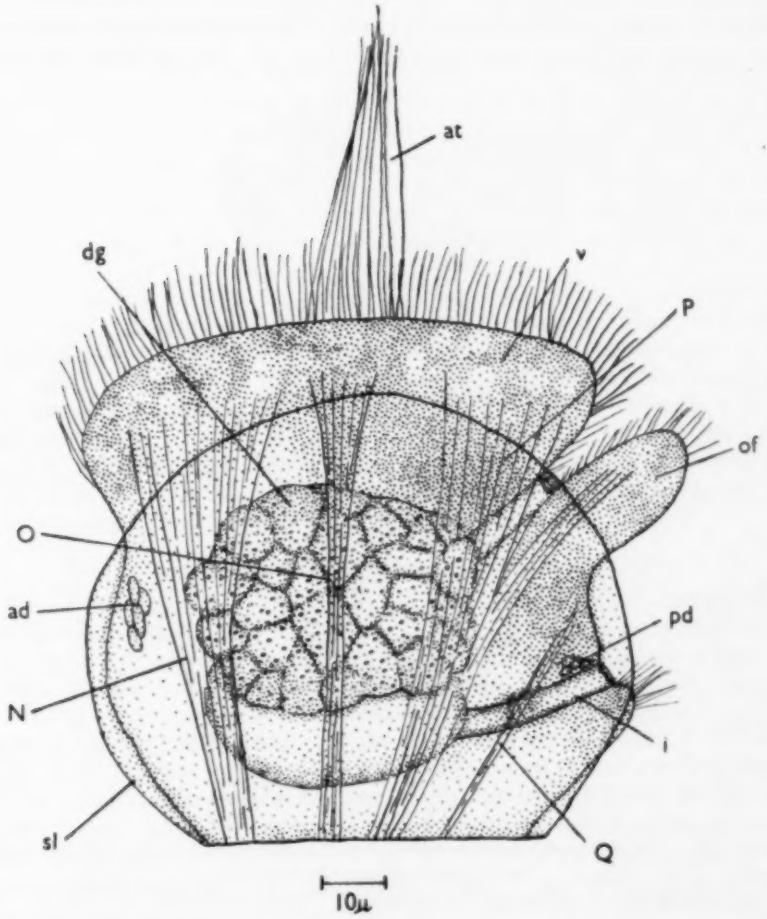

Fig. 4.—Side view of 5 day veliger. ad, anterior adductor ; at, apical tuft of cilia ; dg, digestive gland ; i, intestine ; N.O.P.Q. letters for different pairs of larval retractor muscles ; of, oral flap ; pd, posterior adductor ; sl, shell ; v, velum.

The early veliger stage : (Figs. 4 and 5).

The digestive system:—at this stage the digestive system looks and functions very like that of *Ostrea* (Yonge, 1926). It is still a U-shaped structure but the limbs of the U have become separated by the growth of the epithelium between mouth and anus. The mid-gut sac (the dilatation of the gut from which the stomach and digestive system will form) and the anterior limb comprising the mouth and oesophagus, lie immediately below the velum ; the funnel like stomodaeum opens in the position to which the closed blastopore migrated. Stomodaeum and oesophagus form a wide, strongly marked channel to the mid-gut sac. At this stage the future stomach, style sac and digestive gland are not constricted from one another although histological differentiation is well marked. Large vacuolated digestive gland cells which are a conspicuous green or yellowish brown depending on the food, form the lateral and ventral walls ; elsewhere

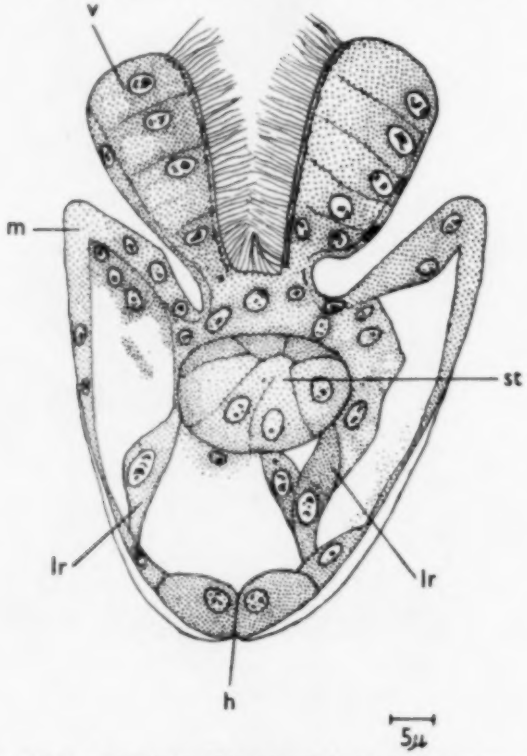

Fig. 5.—L.S. 3 day veliger near anterior adductor muscle and in the region of the most anterior pair of larval retractor muscles.

h, hinge line ; lr, larval retractor muscle ; m, mantle ; st, stomach ; v, velum ;

the walls are flattened and strongly ciliated. The ciliary currents in the sac are very powerful and cause rapid rotation of small flagellates and other contents during life. The intestine leaves the stomach on the posterior side. It is a

short narrow structure but even at this stage shows a kink where it will become much convoluted later. Its walls are thin, and closely applied around them are a few undifferentiated mesoderm cells from which the reno-pericardial complex will develop.

Between the trochophore and veliger stages the velum begins to develop the flattened lateral lobes characteristic of the late veliger stage and as the larva elongates the whole region becomes elliptical in surface view. Histologically the cells become larger and more vacuolated and their cilia thicker and longer. In the centre of the velum a thickened mass of cells develops around a depression in the surface. From cells around the depression emerges a tuft of exceptionally long cilia, which beat in unison. The way they move and precede the animal, pointing in the direction in which it is swimming, suggests they have a sensory function.

The young veliger has three modes of swimming. Most commonly the velum is fully expanded and its cilia drive the larva along in anti-clockwise circles. However if the animal has been disturbed it may swim in another way —the velum is retracted but the shell valves remain open so that the beat of the velar cilia causes slow movement. The third method of swimming has been observed but rarely and then only for a short time. The velum is turned so it is held at an angle to its normal position and the larva moves slowly and obliquely.

In the trochophore the shell gland formed a plate of cubical epithelial cells on the future dorsal surface. The majority of these cells have flattened, elongated and spread over the sides of the larva by the early veliger stage. They secrete shell valves, one on each side. Two rows of cells along the mid-dorsal line, the future hinge line, do not flatten so rapidly (Fig. 5). Extension of the shell gland cells over the sides of the larva is followed by the formation of a pair of lateral folds along the line where the shell gland tissue adjoins ordinary epithelial cells. These folds, visible in a two-and-a-half day larva, are the rudiments of the mantle folds.

Development of the veliger from three to twenty days.

During this time the larvae grow rapidly, increasing from an average length of 80 μ to about 250 μ. Growth varies considerably between individual larvae of the same age even within the uniform conditions of the plunger jars. A similar variation in size was noticed amongst free veligers (Lebour, 1938).

Four to ten day veligers have the D-shaped shell halves characteristic of almost all known lamellibranch veligers ; after this prodissoconch II develops (Rees, 1950) but has no characteristic features except that the length and breadth of the shell are almost the same. No ribs develop during pelagic life.

Although the larva doubles its size during this period differentiation proceeds slowly. The most obvious change is in the velum which grows rapidly and becomes slightly lobed. A small protuberance of vacuolated and ciliated cells, similar to those on the edge of the velum, develops on the ventral lip of the mouth when the larva is three or four days old. This is the oral flap. The digestive system finishes its rapid period of differentiation after a few days development and then differentiates more slowly even though its size increases.

At four days the mouth and oesophagus form a wide funnel-shaped structure down which a strong ciliary current conveys small particles to the mouth. Within the stomach the style sac and gastric shield are recognisable and so is the region from which the digestive gland will grow. The last comprises two laterally placed areas of enlarged cells which are broadly connected with one another by a ventral strip of digestive gland cells. They become increasingly constricted from the gastric portion from the eight day but do not have separate openings into the stomach in the veliger stage. The intestine remains short, developing only a single bend which lies against the side of the stomach.

Development of the nervous system is very slow in spite of the co-ordinated movements of the larva and its ability to contract rapidly into its shell from the fifth or sixth day. At about three-and-half days an invagination of cells in the centre of the velar area indicates the development of the apical pit. This lies immediately adjacent to the apical tuft of cilia. The cerebral ganglia are delaminated from cells on either side of the apical pit. There is no trace of delamination of sub-oesophageal pleural ganglia which might fuse with the cerebrals. By twenty days there are compact well developed cerebral ganglia lateral to the apical pit and dorsal to the oesophagus, which they touch in contracted animals. No other ganglia are delaminated until metamorphosis begins.

The reno-pericardial system is represented throughout the larval period by a few cells lying close to the wall of the rectum. At twenty days there is no trace of a foot in most specimens ; in a few there is a slightly indented protuberance between mouth and anus.

The anterior adductor muscle develops precociously and is a relatively thick structure by four days. The posterior adductor develops more slowly.

The lateral folds from which the mantle develops increase in length and soon envelop the greater part of the body. Their cells become so elongated and closely pressed together that the mantle lobe looks as if it is one cell thick at about seven days, but the ventral edges of the mantle always remain thickened and form two lobes during the veliger stage as in *Venerupis pullastra* (Quayle, 1952).

The first pair of gill filaments begins to develop at about seventeen days when thickened masses of cells arise posteriorly in the angle between the body wall and mantle.

No larval excretory organs are found.

The larval retractor muscles (Fig. 4)

The function of the larval retractor muscles is to contract the whole body of the larva so that it can be enclosed with the larval shell. They develop early : two pairs (N and P) begin to differentiate when the larva is between thirty-six and forty hours old, and eight to ten hours later extend from the region where the hinge is forming to the velum. One pair is on the side where the future anterior adductor muscle is differentiating, and the other, on the larval ventral surface, extends from the hinge to the part of the velum near the stomodaeum. At this stage the retractors consist of two or three elongated cells which are not contractile. They divide and differentiate so that by the end of the third day they can pull the veliger within its shell.

On the third and fourth day of development a third pair of retractor muscles (O) develops between the other two. These also originate near the hinge line ; they extend to the central region of the velum on either side of the apical pit (Fig. 4). By six days these three pairs of retractor muscles are fully developed and in whole animals one can also see two or three elongated cells (Q) extending from the hinge line to the epidermal cells between mouth and anus, the region where the foot will develop. This pair of retractor muscles does not develop fully until the veliger is older. Once the foot develops during the late veliger stage the larval " foot " retractors lie close to the differentiating adult posterior pedal retractors ; the latter are easily distinguished since all their fibres decussate, while those of the larval muscles do not. In this group of four pairs of muscles, two pairs N and O (Fig. 4) are inserted into velar cells, one pair (P) is inserted into stomodael and velar cells ; and the fourth pair Q run from the hinge, first to the presumptive foot epithelium and later to the developing foot itself. It seems reasonable therefore to follow Crofts (1955) and call them larval retractor muscles although they differ from the larval retractor muscles she describes in *Haliotis* because each separate muscle comprises a number of small cells. They are lost together with the velum at metamorphosis.

The larva at metamorphosis (Fig. 6)

After about three-and-a-half weeks of pelagic development the veliger sinks to the bottom and metamorphoses to an adult. Artificially reared specimens are approximately 270 μ long by this time and " free " ones 250-350 μ long (Jørgensen, 1946). The velum is a large structure and functional until the larva has settled.

Internally the adult organs, apart from the digestive system, are little differentiated although the growth of the foot and gills proceeds rapidly during the last week of pelagic life. During this time four pairs of gill filaments develop and these become ciliated while short knobs of tissue. The foot develops by proliferation of the mesodermal and epidermal cells between mouth and anus. Within the protrusion so formed, some cells, delaminated from the epidermis on the anal side, form the differentiating pedal ganglia. Some of the mesoderm cells of the foot together with others in the body cavity differentiate into posterior pedal retractor muscles before settling occurs. The statocysts develop from a pair of epidermal invaginations dorsal to the delaminating pedal ganglia. They are cut off from the epidermis and have secreted statoliths within a short time of settling. At this stage the tip of the foot is ciliated and bears a deep invagination—the rudiment of the pedal gland.

At metamorphosis there is no reno-pericardial system. and the cells around the rectum from which it will arise are few and not readily identified. In the anterior part of the larva, the velar plate region increases in size a little at this stage and the nuclei of its cells and those in the cells forming the cerebral pit become prominent and stain deeply with nuclear stains.

Development of the spat

Three weeks after settling the spat are still small, 600-700 μ long, but they are more easily recognizable as young cockles since the most recently formed

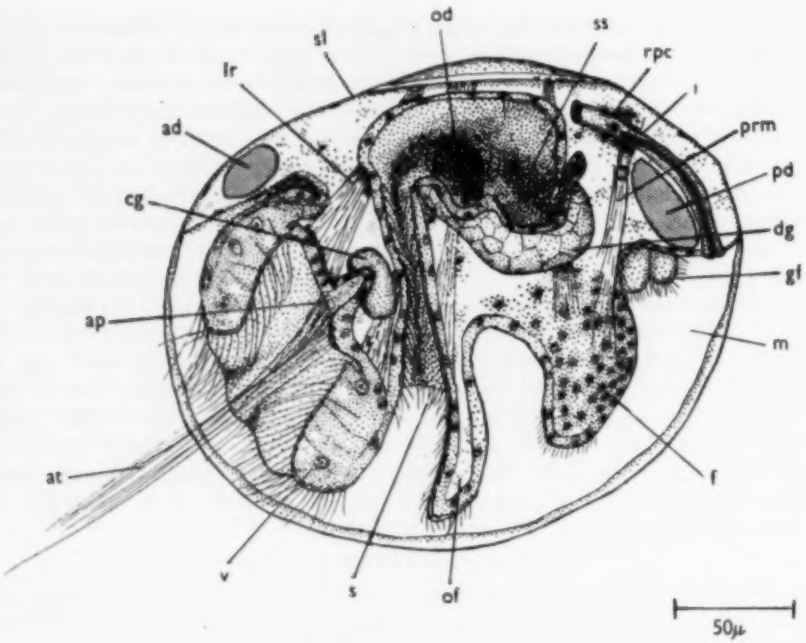

Fig. 6.—Reconstruction of right half of 25 day *Cardium* veliger.
ad, anterior adductor ; ap, apical pit ; at, apical tuft of cilia ; cg, cerebral ganglion ; dg, digestive gland ; f, foot ; gf, gill filament ; i, intestine ; lr, larval retractor muscle ; m, mantle ; od, opening of right digestive gland lobe ; of, oral flap ; pd, posterior adductor ; prm, posterior pedal retractor muscle ; rpc, future reno-pericardial tissue ; s, stomodaeum, sl, shell ; ss, style sac ; v, velum.

shell is ribbed and the shape of the shell is similar to that of the adult. Prodissoconch II is still present and forms a large portion of the shell.

It is during the early settlement stages that the stomach develops the angle between its two principal regions which is characteristic of the adult. The anterior part which is small in the veliger, increases in size relative to the posterior and ventrally projecting style sac. The digestive gland enlarges on each side of the anterior region so that its two lobes cover the lateral surfaces, extend dorsally towards the hinge and, to a lesser extent, ventrally into the foot. In recently settled specimens the lobes still have a common and comparatively large opening into the antero-ventral side of the stomach. Posterior to the digestive gland opening is a well developed gastric shield with the thickened " tooth " typical of the adult. The ciliated style sac is also well developed and grows into the dorsal part of the foot as the latter develops. The intestine still has a single anteriorly directed loop on the right side of the dorsal part of the stomach.

The reno-pericardial system differentiates in the posterior region of the animal between the posterior adductor muscle and the posterior end of the stomach. The kidneys develop first. Six weeks after fertilization the kidney

rudiment comprises two wedge-shaped structures on either side of the rectum. These fuse medially below the rectum, although at this stage there is no communication between their lumena. Each kidney has a vacuolated cubical epithelium bordering a small lumen and each opens into the postero-dorsal part of the mantle cavity by a short narrow duct from the ventral surface. The pericardial rudiment is less developed and comprises a layer of differentiating cells surrounding the rectum dorsal to the kidney tissue.

Ventral to the kidney rudiments the visceral ganglia are delaminated from epithelium in the posterior region of the mantle cavity. They differentiate rapidly and by the time the cockles are seven weeks old are connected to each other and to the rest of the nervous system.

Within the foot the anterior pedal retractors develop within the first few days of settling when the animal is about four weeks old.

The cerebral pit and velar lobes disappear immediately after metamorphosis. Development of the palps was not studied in detail but from the sections examined, the velar area surrounding the cerebral pit develops into the anterior pair of palps as it does in *Ostrea* (Cole, 1938). About ten days after settling the anterior palps on each side are differentiating rapidly in the region formerly occupied by the apical plate and the appearance of the cells in this new pair of structures, with their deeply staining nuclei, is similar to that of the apical plate cells immediately before metamorphosis.

Spat of *Cardium edule* were examined again during their first autumn about three months after they had metamorphosed. At this stage they are between 0·75 mm. and 1·5 mm. long, their shells have the adult shape and are ribbed except at the umbones which are formed by the persistent prodissoconch II.

The stomach of the adult cockle was described in detail by Graham (1949) so it was examined to see whether the structures he described had developed. The wide funnel-like mouth has two pairs of well developed labial palps lateral to it and lies close and ventral to the anterior adductor muscle. It is connected to the stomach by a short strongly ciliated oesophagus. The main structures in the stomach are similar to those described in the adult but the elaborate ciliated folds are not present in their adult form. There are the two distinct regions: an anterior globular part which contains the gastric shield and the openings of the digestive gland lobes, and a ventrally projecting portion which comprises the style sac and the intestinal groove. The latter lies on the anterior side of the style sac.

Graham (1949) describes the globular region of the stomach as having four structures opening into it ; the common opening of the right digestive gland ducts, the common opening of the left digestive gland ducts, the caecum (an antero-ventral pouch of the stomach) and the dorsal pouch. All these openings are lined by stomach epithelium. In 1·0 mm. spat the left digestive gland lobe is almost completely divided into separate dorsal and ventral lobes, the right lobe is still single. Right and left lobes open separately into the stomach and their openings are separated ventrally by a ciliated tract of cells. This contrasts with veligers about to metamorphose in which the two digestive gland lobes are not separated at all ventrally. A slight evagination of the ventral

wall of the globular portion of the stomach may represent an early stage in the development of the caecum. The digestive gland openings are separated dorsally by another tract of ciliated cells. This extends from the edge of the gastric shield posteriorly to the oesophagus anteriorly. Along its path a slight dorsal evagination probably represents the initial stages in the development of the dorsal pouch. The dorsal and ventral ciliated tracts are linked on the right wall of the stomach by ciliated epithelium on the posterior side of the opening of the right digestive gland lobe. The gastric shield, a relatively broad sheet of hard secretion lies on the left side of the globular region of the stomach, posterior to the opening of the digestive gland lobe and dorsal to the style sac. The intestine is still relatively short.

The pericardium and heart differentiate rapidly during the first two months of settlement, and in 1·0 mm. spat pericardium and heart are in their adult condition. The pericardium and developing kidneys touch one another along the middle region of the ventral wall of the pericardium. The two kidney rudiments are completely fused and have a large common lumen. They open to the exterior by two ventrally directed ducts each of which is lateral to the visceral ganglion of its own side. Each kidney duct is very wide dorsally but tapers to a tiny pore at the place where it opens into the mantle cavity. The greater part of the funnel-like duct is composed of vacuolated kidney cells. There is a renopericardial duct from each of the original kidney rudiments very near their anterior ends. They run antero-dorsally to open into the ventral side of the pericardial cavity. At this stage the gonads are completely undifferentiated.

The foot is comparatively large and the animal burrows actively. Its anterior tip is ciliated ; posterior to this ciliated region is a median depression into which the pedal gland opens. The secreting part of the gland lies in the posterior part of the foot and comprises a simple sac of vacuolated cells and ciliated cells surrounded by some sub-epithelial glandular cells. Its duct has longer denser cilia than the sac. Anterior and posterior pedal retractor muscles are well developed and these and the intrinsic muscles of the foot form a layer of muscular tissue beneath the epidermis.

Development of the gills was not followed but in 1·0 mm. spat there is still a single row of filaments. The oldest and longest of these, at the anterior end, had the adult type of ciliation and their ventral tips were reflected inwards. Their condition and degree of development is very similar to that in *Venerupis* spat of the same size. At the posterior end of the animal the siphons which arise posterior to the most recently differentiating gill filaments are already muscular and well developed structures.

DISCUSSION

The most striking feature of lamellibranch development is the similarity of the pelagic larvae until the second half of the veliger stage ; even the Taxodonta, whose barrel-like larvae are superficially unlike the rest, differ from the others mainly in the prolongation of the velum into a " mantle " for the rest of the body. Similarity of the veligers is such that identification of the common species is almost impossible until the D-shaped larval shell (Prodissoconch I)

has been replaced by Prodissoconch II. Then the development of the hinge teeth and some approximation to the adult shape make identification more certain (Werner, 1939; Rees, 1950). Early development in *Cardium edule* follows the same pattern as in other lamellibranchs for which it has been described—*Mytilus edulis* (Field, 1922), *Dreissensia polymorpha* (Meisenheimer, 1901), *Ostrea virginica* (Stafford, 1913), *Sphaerium* (=*Musculum*), (Okada, 1935), *Anodonta* (Herbers, 1914) and *Hiatella orientalis* (Miyazaki, 1938b). The first cleavage is unequal and for several subsequent cleavages two large cells persist at the vegetative pole. In *Cardium* and *Dreissensia* the primary mesoderm cell sinks into the blastocoele before gastrulation ; but in *Mytilus edulis* it is said to be enclosed by epibolic downgrowth of the smaller cells. In all cases the inclusion of the future mesodermal tissue within the blastocoele is followed immediately by invagination of the future endoderm.

The rate at which the organs develop after this depends on whether they will be used during the larval period. In free swimming lamellibranch embryos the shell gland develops precociously arising at the same time as the endoderm invaginates. Its precise mode of origin varies—in *Mytilus edulis* and *Cardium edule* a plate of thickened cells is formed on the future dorsal surface, this plate divides into two and in each half the cells become flattened and begin to secrete the shell. In *Dreissensia* the flattening and division of the shell gland cells is preceded by their forming a deep invagination, which looks very similar to the digestive system. Another structure which develops precociously in all free-swimming lamellibranch larvae is the digestive system. This is a U-shaped structure in trochophores and young veligers. Its shape is determined by the development of the future ventral surface, the future foot, which separates the stomodaeum and anus. The foot is represented by a very few cells during the early stages so the mouth and anus at the two ends of the U are very close together. The U straightens at metamorphosis when the foot grows and the velum is lost.

All the common lamellibranch veligers have the same shape of velum and this large structure, together with the rest of the larval body, can be pulled within the shell valves by well developed and paired larval retractor muscles. These larval retractor muscles are similar although not identical in *Dreissensia* (Meisenheimer, 1901), *Mytilus edulis* (Field, 1922), and *Cardium edule*. The paired larval retractor muscles of *Cardium* are inserted round the mouth opening and in the region where the foot will develop as well as in the velum. In this they are similar to the single and asymetrically placed left larval retractor muscle described in four genera of developing Archaeogastropoda by Crofts (1955) and in the opisthobranch *Adalaria* by Thompson (1958). Garstang (1929) suggested that the development of asymmetrical larval retractor muscles was the original cause of torsion in the larvae of the ancestral gastropods ; Crofts modified this hypothesis finding that the pretorsional right (post-torsional left) retractor muscle developed first and suggested that the post-torsional right larval foot retractor muscle which develops much later is its pair. The muscles both develop but at different times. The larval retractors of *Cardium* develop at the same time on both sides of the body and so show the arrangement one would expect in the most primitive molluscan larvae.

Recently Lemche (1959) has suggested that the presence of four pairs of larval retractor muscles in lamellibranch veligers, together with other evidence from nautiloids, indicates that there were four or five segments in the ancestors of the Mollusca. The arrangement of the larval retractor muscles in *Cardium edule* does not entirely support this view :—the arrangement of the three largest pairs of muscles at the two ends and in the middle of the relatively long hinge line (Fig. 4) is what one would expect for functional efficiency ; the development of the velum has obscured the exact relationship between the larval muscles and the antero-posterior axis of the animal since the mouth has been displaced towards the anus ; also the major part of the larval musculature is concerned with the retraction of the velum, a structure which must have developed from pre-oral tissue, and all the retractor muscles are lost when the velum disappears at metamorphosis. On the other hand two factors supporting the idea that the larval retractor muscles indicate the arrangement of ancestral segmental muscles are the separate origins and development of each pair of muscles, and the way that each muscle consists of several small muscle cells.

Quayle (1952) has given a full account of the development of the heart and kidneys in *Venerupis pullastra* and the development of these organs follows a similar course in *Cardium*, and is similarly delayed until metamorphosis. The main difference between them is that in *Cardium* the pericardial and renal cavities are connected by a pair of short and simple ducts, but in *Venerupis* they are connected by elongated structures which run within the kidney for over half their length. In both these marine species there is no larval kidney and the adult kidney cells are not fully developed and functional until after the spat have settled. The metamorphosis which occurs at settlement therefore involves the differentiation and rapid growth of the adult reno-pericardial, nervous and muscular systems, as well as the loss of the velum and the development of gill and siphons.

SUMMARY

The ova and sperm of *Cardium edule* develop in the gonads between October and March. They are shed at the end of May, the exact time of spawning depending on air and sea temperatures.

Ova must be mature before fertilization is possible. Most fully developed testes have some mature sperm.

Cleavage is unequal and, of the four macromeres at the eight celled stage, two are much larger than the others.

The mesoderm mother cell sinks into the blastocoele before gastrulation and the latter process is brought about by invagination aided by an increase in the area covered by the small ectodermal cells of the animal pole.

The digestive system, shell gland and prototroch differentiate so rapidly that seventy-two hours after fertilization the veligers are swimming actively in the water.

After four to five days development the anterior adductor and larval retractor muscles are functional. The larval retractor muscles are paired and are attached proximally near the hinge line, and distally to the velum, the oesophagus and the epithelium of the presumptive foot region.

The style, style-sac and gastric shield are developed within the first five days but the elaborate folds of the adult stomach are not fully developed until some months after metamorphosis.

During the pelagic stage there is rapid growth (from 60 μ to 350 μ in length) but, after the first four days, there is little further differentiation until the larva are three weeks old. Then the nervous system, foot, muscles and gills develop rapidly. This second period of differentiation continues after settlement when the reno-pericardial system and ultimately the gonads develop.

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THE IMMOBILIZATION OF AFRICAN ANIMALS IN THE FIELD, WITH SPECIAL REFERENCE TO THEIR TRANSFER TO OTHER AREAS (U.S. TRANSLOCATION)*

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(With 4 plates)

The need for urgent measures to preserve African game for study and assessment of ecological importance is briefly discussed. The use of paralysing drugs for the capture of these animals is described. The applicability of the method for the transfer of animals threatened by poaching, farming and other agrarian activities is dicussed, together with problems associated with removed populations.

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INTRODUCTION

The preservation of African wild life is a matter of the greatest concern. The rate of destruction of animals in this country has reached such proportions that unless strenuous efforts are made, the majority of large species may be almost extinct within a generation. Even the existence of game parks does not completely safeguard larger animals, whose normal migratory habits are increasingly curtailed, and so may ultimately be deprived of essential food stuffs.

It is desirable to preserve African wild animals, not only for aesthetic and scientific reasons, albeit many would consider these adequate, but also for their possible importance in the proper use of land.

Large scale and permanent destruction of land by wasteful and erroneous methods of arable and stock farming has been and is a matter of concern in many countries, and there is an increasing tendency to reserve large tracts of land in a state of natural balance to act as catchment areas and as barriers against erosion. These natural areas can be made productive by controlled

*Based on a paper read at the Sixth British East and Central African Fauna Conference, Northern Rhodesia, August 1959.

game cropping, under careful management, to yield valuable protein and also as a source of revenue as controlled hunting areas. A particularly African problem is the spread of bush which is steadily encroaching on considerable areas in East Africa alone. It is well known that many of the larger species—giraffe, eland and rhinoceros—are browsers and feed on this type of vegetation ; their reduction may well contribute to this serious spread. It is a slightly hopeful trend that in some areas where game has been exterminated, there is an increasing demand by farmers to have their land restocked with wild antelope.

It is certain that the value and position of these animals in the economy of the country is not known. In the absence of agreed and extensive policies directed to the proper use of wild life and natural resources, one of the urgent problems concerned with the preservation of wild animals is their removal from areas where they are not tolerated, to places of greater safety. In the past, the control of animals in real or apparent conflict with man has been through destruction, by poisoning, shooting or snaring. More recent attempts to capture them by driving and netting, with the object of removing them from specific areas, has failed, particularly as far as adult animals are concerned. Either the animals will not be driven, or a high mortality attends their capture in nets due to fright and the necessary force to control them.

METHODS

The technique of paralysing animals by the use of drugs offers a humane and practical alternative to former methods. The marking of animals as a means of study has been considered desirable for a decade (Worthington 1950) and the use of paralysing drugs for this purpose envisaged at least as early as 1956 (Kinloch 1956). Recently this method has been developed into a practical technique (Crockford *et alia* 1957). A drug, for example nicotine salicylate, is administered by a dart or automatic syringe delivered to the animal by a gas powered gun. The animal, paralysed by the drug, can then be marked with an identification disc or ' tag ', and its subsequent movements recorded.

This technique has greatly facilitated the study of wild animals their migration cycles, birth and death rates.

Grzimeck in 1958 (Gimbel 1959) used this technique for marking several species in ungulates in the Serengeti National Park and it has been used in Uganda for the study of the kob (*Adenota kob thomasi*) (Buechner 1959). This method was later adopted for the capture of animals for their transfer.

A preliminary stage in this work is the investigation of suitable drugs and doses for a wide range of animals.

For smaller species nicotine salicylate is undoubtedly effective, but has many disadvantages. It is extremely toxic, dangerous and unpleasant to handle, and the recovery of the animal may take as long as four hours. Also its effects on the animal are such as to lead us to deprecate its use on humanitarian grounds.

Succinylcholine chloride has been investigated on a considerable number of species and a preliminary report has been prepared (Buechner, Harthoorn & Lock, 1959). Since this report paralysing doses have been found for the hippopotamus (*Hippopotamus amphibius*), namely 0·1 milligram per kilogram, and the buffalo (*Syncerus caffer*) at 0·055 milligrams per kilogram. The addition

of atropine, 0·11 milligrams per kilogram, was found essential for this animal. In the absence of atropine, excessive bronchial secretion, provoked by the paralysing drug, caused death. d-Tubocurarine was also tried on buffalo and the drug was found to be effective when combined with atropine. It had, however, the disadvantage of slow onset of paralysis—about forty-five minutes—recovery taking place in one hour. Succinylcholine, with all species so far tried, produced paralysis in about ten minutes, recovery occuring within half an hour. This is of course an important factor where animals may seek cover before the onset of paralysis.

Considerable species variation is shown in the response to the drug. Kob (*Adenota kob thomasi*) and waterbuck (*Kobus defassa ugandae*) may be paralysed completely with a certainty of recovery. Hippopotamus are best given a dose which renders then incapable of walking, but leaving other bodily activities, including jaw movements, little impaired. Since for identification of individuals, hippo are probably better branded than earmarked, this is no disadvantage.

The black rhinoceros (*Diceros bicornis bicornis*) and elephant (*Loxodonta africana*) have both proved difficult subjects. Early attempts were abortive, largely owing to needles of inadequate length. The hard skin of the rhinoceros tends to damage the syringes used, but indications are that successful injections may be made in the neck and hump and an effective dose has been found. Complete success has not yet been achieved with the elephant, but indications are that the effective dose is a little under 0·70 milligrams per kilogram.

Much remains to be done before this aspect of the work can be considered complete; particularly other drugs and adjuvants are to be tried to increase the margin of safety, especially since, for general field work on a large scale, people not trained in accurate dispensing may have to be employed.

Following successful paralysis, animals are then captured, given, if necessary, a suitable tranquillizing drug, and conveyed to other areas. Possibly this method is equally suitable for capture for zoological gardens.

APPLICATION

In June 1959 we moved two female kob 75 miles from Lugari to West Suk in Kenya, demonstrating that the method is practicable. The tranquillizing drug used was Largactil (chlorpromazine) given in a dose of 2·2 mg. per kilo, and the animals were handleable and apparently unfrightened by the experience. This trial has provided some of the necessary knowledge for the removal of 200 to 300 kob from the Lugari farming area, which is the only place they now exist in Kenya, to suitable habitats elsewhere in the country. During the same field operation it was also demonstrated that the Rothschild giraffe (*Giraffa camelopardalis rothschildi*), could be immobilized and six of these rare giraffe now wear ear tags and are under observation for possible undesirable after effects. It is planned to move twenty-five of these animals to the West Suk where their behaviour and health will be observed. If this pilot experiment is successful, and the animals seem to become established in the new surroundings, further groups will be removed to the same area leaving behind only a small number compatible with farming interests.

Ten years ago about 1000 black rhinoceros were shot in the Makeuni area of Kenya prior to native settlement. Further bush will have to be cleared and it is hoped to avoid shooting by transporting at least a proportion of these animals, also heavily threatened by poaching, to the Northern Frontier Province.

Lessons learnt from the black rhinoceros may be applied to the rare white rhinoceros (*Ceratotherium simum cottoni*) and it is hoped ultimately to remove some of these from the West Nile district of Uganda, where they are at present heavily poached, to a National Park.

The inoculation of wild animals with rinderpest vaccine has also been shown to be a practicability at least in National Parks (Harthoorn & Lock 1959).

Much work remains to be done before the value of these methods can be assessed for the large scale control of game. For example transferred populations must be studied for their establishment, balance with predators, rates of increment, weight gains and possible interbreeding with subspecies.

Although the killing of animals under a system of controlled cropping and shooting for protective reasons must continue, it is hoped that methods of immobilizing and transporting animals will contribute materially to the preservation, proper use and study of wild life in Africa.

ACKNOWLEDGMENTS

We express our gratitude to the Game Department, Uganda for co-operation and assistance in the purchase of materials ; to the Kenya Game Department and Uganda National Parks for co-operation ; to Burroughs Wellcome, East Africa, Ltd., for gifts of succinylcholine and May and Baker Ltd., for the gift of Largactil in specially concentrated form ; to the Palmer Chemical and Equipment Company Inc., U.S.A., for gifts of equipment and chemicals.

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Fig. 1.—Young male Uganda kob. Showing easy handleability under the influence of Succinylcholine. Semliki Valley, Uganda.

Fig. 2.—The kob gets to its feet. Note marker on ear.

Fig. 1.—The kob runs to rejoin the herd.

Fig. 2.—A Rothschild giraffe recovering. (Kapenguria, Kenya 1959). Note marker on ear.

Fig. 1.—Hippopotamus. Not completely immobilised, but incapable of walking. (Kazinga Channel area Uganda. November, 1959.)

Fig. 2.—The hippopotamus goes off to water. Note plastic marker on tail.

Fig. 1.—Buffalo going down under the influence of the drug. (Queen Elizabeth National Park, Uganda, November, 1959.)

Fig. 2.—The buffalo rising to his feet. Note marker on tail.

ON THE RETRIEVING OF YOUNG AND OTHER BEHAVIOUR IN LACTATING GOLDEN HAMSTERS

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(With 12 figures in the text)

The behaviour of females at all stages of lactation on finding a strange pup in her cage is described. Pups between seven and fourteen days old are most likely to be retrieved rather than attacked, but factors dependent on the time since the female gave birth also govern her response.

To separate these latter factors into those dependent on the age of the litter and those dependent on internal changes in the female, parts of the retrieving pattern were timed in mothers retrieving their own pups. Some of these animals were living with their own litters, others maintained foster litters of roughly constant age throughout lactation. It was found that the type of behaviour shown depended only on the age of the litter at the time.

Although the foster litters did not grow older and therefore change in their milk requirements, foster mothers did not go on lactating longer than normal. The time they spent away from the nestlings also changed in the normal way. It was concluded from this that the foster mothers were not affected physiologically by their litters.

The relevance of the concept of maternal drive in discussing these factors is considered, and it is concluded that it does not help to explain them.

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INTRODUCTION

The overt behaviour of the mammalian mother towards her offspring has received comparatively little attention, though her physiology, and the behaviour and development of her young are well studied. Several workers have assumed a maternal drive causing her behaviour, and attempted to measure it by means of maze or barrier techniques. Wiesner & Sheard (1933)

pointed out fallacies in the design of these experiments, which did not take into account change of stimuli from the young as they grew older. They made observations on changes in the maternal drive of the albino rat, using retrieving of pups of different ages by both lactating and non-lactating animals as their criterion. Seward (1940) assessed changes in maternal drive in the guinea pig, using a barrier technique, and found a " general decline in drive strength " during lactation unaffected by change in age of young or pressure of milk in the glands. Like other workers he assumed that (man always excepted) maternal behaviour towards appropriate objects is only shown when the animal is influenced by hormones appropriate to the mother animal—usually progesterone and prolactin ; this specific hormone action is an important basis of " maternal drive ". There is, however, a body of literature describing maternal behaviour shown by normal male, virgin female and juvenile mammals which is difficult to reconcile with this assumption (Beniest (1958), Horner (1947), Rowell, (1960)). An allied theory of the origin of maternal drive emphasises the physiological effects of prolactin and associated hormones and assumes that maternal activities are directed towards the goal of reducing tension in the mammary glands (*e.g.* Lehrman (1956)). The work of Beniest and others does not support this theory either, since the non-maternal animals were not lactating and there was therefore no mammary tension to be reduced. Bacq (1932) showed that although his sympathectomised rat did not lactate properly, she was nevertheless as assiduous in the care of her litter in other respects as other mothers. In this animal not only were the mammary glands at less than normal lactating tension, but the nervous pathways through which information about the tension would normally be transmitted were destroyed. Leblond & Nelson (1936) hypophysectomized rats at parturition, and these animals did not lactate, but again they showed full maternal behaviour towards their litters. Some of the conflict of views on these points is apparently due to interspecific and interstrain differences in the amount of maternal response shown by non-lactating animals.

The sensory determination of behaviour towards young was studied by Beach & Jaynes (1956) in the albino rat ; they concluded that several modalities were involved in recognition, including smell and touch, but probably not sight. Unfortunately they made no provision for auditory cues : Zippelius & Schleidt (1956) have shown that murine nestlings taken out of the nest give a special ultrasonic cry which is a very powerful stimulus to the mother rat or mouse, causing her to seek for and retrieve the pup.

It seemed that a study of the occurrence of maternal behaviour in a species, and of the objects to which it was directed, using normal healthy animals, was necessary. The experiments described here deal with lactating golden hamsters. Changes in some aspects of their maternal behaviour with time, and when pups of various ages are the objects of the behaviour, are analysed.

MATERIAL AND METHODS

The animals

The female hamsters lived in cages made of wire, 2 feet × 1 foot × 1 foot in size, with fine mesh wire floors. A glass fronted wooden nest box with a 2

inches diameter entrance hole in one side was fastened to the front of each cage. The animals made nests in these boxes with hay provided, and eventually littered there. Mothers from the first day to thirty days after parturition, and pups up to thirty days old were used in the tests. As the experiment proceeded, however, it became apparent that after twenty-six days one is dealing with weaned families, and that these are not necessarily a social group comparable with the suckling litter and mother. The results from twenty-seven to thirty days have been included, however, since in the aspects studied they do show a reasonable continuation of the trends seen in earlier groups.

The behaviour pattern analysed

Retrieving is the response of the mother to the situation " young outside nest ". She may find the pup by orienting to the very high frequency "fffff-ffff-ffff" cry given by a chilled pup ; or she may first see, smell or touch it. Typically she then picks it up and carries it between the incisors to her nest, drops it amongst her litter, licks it, and then either gives the suckling posture or goes out of the nest again apparently to look for more stray young. This is a constant pattern which can easily be described quantitively and qualitatively, and unlike most aspects of maternal behaviour it can be elicited at will within the framework of the normal experience of the mother, since one of her own pups may (at least in captivity) get out of the nest and need retrieving at any time. In this type of behaviour study it is important that any experiment should appear to the animal as an unremarkable part of daily routine.

Procedure

All observations were made during the first four hours of darkness, which is the time of maximum activity in the golden hamster. (The colony lived in a reversed daylight regime so that this period occurred in normal working hours.) Test pups were always transferred by hand. The animals were all accustomed to being handled by the experimenter, and there is no evidence that handling pups affected behaviour shown towards them (except during parturition, which is not discussed in this paper). Test pups were kept if necessary in a warm place after being taken from their home nest until the mother to be tested was brooding in her nest, or the mother of an older family had her attention sufficiently distracted for the pup to be placed unnoticed in her cage. Recording started when the mother was seen to be alert and continued until she ceased to show interest in the pup. In some cases the test pup was weighed before being offered.

For some test series foster families were used. On the second day after birth the litter was exchanged for one of six, ten or fourteen days (as nearly as possible with the available stock) and was thereafter exchanged every four days so that the mother maintained a litter of nearly constant age (within four days) throughout her lactation. Some mothers kept their own litters for six days and thereafter maintained two to six day litters. Each litter, of three to five pups usually, was fostered by successive mothers until eighteen days, a

regime which was bad for them and sometimes produced a certain amount of backwardness, but the ideal procedure of using each litter for only one four-day foster period would have required a reserve colony of considerable size for which there were no facilities.

REACTIONS TOWARDS STRANGE PUPS

It was observed that a mother would readily retrieve one of her own pups, or a pup of the same age from another litter, when presented to her as described. On the other hand she would attack young adult hamsters, using the methods appropriate to a territorial rival, and young rodents of other species were treated as prey. (Hamsters, like many rodents, are carnivorous when opportunity offers.) Some preliminary tests were therefore carried out to discover what a pup, in the sense of " an object to be retrieved ", meant to females at various times after parturition, that is, how they behaved towards pups of different ages. Age combinations of test pups and own litters were determined only by the ages of litters available at the time.

Observations

The following behaviour patterns were observed :

Mother	*Test pup*
Retrieving (full pattern)	" Crawling under "
Carrying	" Puffing "
Uncompleted picking up	Squeaking
Licking	Tail up (submission)
General investigation	" Submissive posture "
Anogenital investigation	Suckling
Toleration	
Attacking (as rival)	
Killing and eating	
Lordosis	
Violent or hurried grooming	

Although the behaviour of the mother is the primary interest that of the pup must be mentioned since it may affect her response. Before their eyes open, the behaviour of test pups does not differ from that shown in their own mother's cage. Shortly after, they begin to recognize the strangeness of the situation, and react to the female's investigations differently : crawling under the larger animal (and often out between her hind legs so that she has to turn towards it again). This behaviour is like the behaviour of very young pups towards any large warm object except that there is no attempt to suckle. It is very rarely followed by attack on the part of the larger animal, but usually by retrieving or attempted retrieving even by animals showing some signs of incipient attack. Other older pups investigate the strange cage with erect tail indicating mild alarm, and may panic and flee when investigated by the female or " misunderstand " her attempts to pick them up for retrieving as an attack. A pup which runs away is frequently attacked, but fortunately such individuals were rare and flight cannot be considered the only cause of attacks on pups.

Classification of the tests

For the purposes of analysis the tests were divided into three groups.

i. Acceptance of the pup as object equivalent to own young. This included retrieving of young pups and incomplete retrieving or toleration in the case of pups which were too large to be retrieved.

ii. Rejection. This included killing (as prey) and also attacking as a conspecific rival, which involves quite different movements. Attacks were often preceded by prolonged sniffing and following of the pup interspersed with pauses for rapid grooming bouts which probably indicated a conflict in the female's attitude towards the pup. (Lordosis and anogenital investigation also indicate that the pup is in some measure being treated as an adult, but these two activities were not scored. The first was rare, the second difficult to distinguish from general investigation.)

iii. Ambivalent response. This included those tests in which both the above types of behaviour occurred in about equal proportions ; for example the mother of a two day old litter given a sixteen day test pup retrieved it and later killed it when on her return she " found " it in her nest.

Results :

The tests and their results are shown diagrammatically in Fig. 1. In the upper right hand corner of the diagram, representing tests with older pups

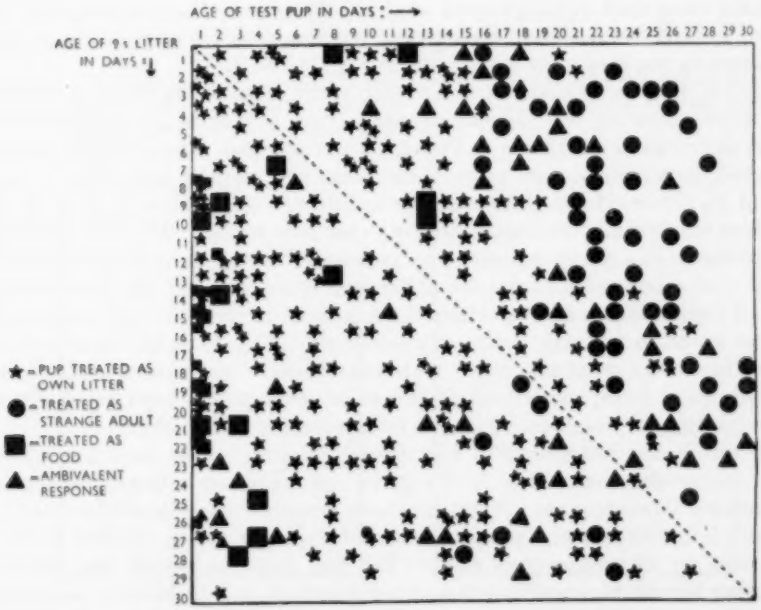
AGE OF TEST PUP IN DAYS
AGE OF ♀'s LITTER IN DAYS
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
= PUP TREATED AS OWN LITTER
= TREATED AS STRANGE ADULT
= TREATED AS FOOD
= AMBIVALENT RESPONSE

Fig. 1.—Results of tests in which strange pups were offered to lactating females. Distribution of the types of response given by mothers in relation to age combinations of strange pup and her own litter shown diagrammatically.

and neoparturient females, the minimum of tests were carried out because they almost invariably resulted in the mutilation of the test pup.

i. No difference was found between the behaviour of primipares and multipares, and the proportions of acceptances, rejections, and ambivalent responses shown by the two groups were almost identical.

TABLE 1

Numbers of primipares and multipares tested, and the responses they gave, expressed as percentages of total tests.

	Totals	Accept	Reject	Ambivalent
Primipares :	142	72	20	8
Multipares :	270	72	19	9
Totals :	412			

(15 tests were not classified as to experience of female.)

ii. The type of " rejection " shown was sharply divided according to the age of the test pup involved : no animal under fourteen days was treated as a rival, and none over that age was treated as food. The most striking change which occurs at this age is the opening of the eyes, which might possibly cause the difference in response indirectly, by affecting the behaviour of the pup.

iii. For further analysis the tests were divided into groups according to age of test pup and time since parturition for the female. The groups used were divided at four day intervals (except for days 1 and 2) and corresponded roughly to easily recognized developmental stages of the pups. The proportions of the three types of test results in each group were expressed as percentages and are represented graphically as histograms in Figs. 3 and 4.

In Fig. 1 it is seen that there is overlap in the areas of the diagram in which the three types of test results appear. Two hypothetical interpretations of the distribution are shown in Fig. 2. The first, (2a), assumes that mothers accepted for the most part pups of the same age as their own litter, with a spread on either side of diminishing probability of acceptance as the test pup becomes more readily distinguishable from her own young. Thus the likelihood of females in any group rejecting any pup could be represented as a U-shaped curve with a minimum at the age of her own litter, and Fig. 3a represents the sum of eight of these curves, where the minimum of the sum happens to occur at the seven to ten day group. Alternatively, Fig. 3a might represent the degree to which a set of unknown " maternal releasers " are present in the various age groups of pups, the stimuli presented at seven to ten days being optimal for retrieving, in which case Fig. 1 is interpreted as in Fig. 2b.

Since all the histograms in Fig. 4, each showing which pups are rejected by mothers whose own litter is of a given age-range, are different, the second hypothesis is inadequate : if the mother's response were dependent only on stimuli from the test pup the proportion of pups of any age rejected would be the same for all groups of mothers. The first four histograms (Fig. 4) would fit either hypothesis equally well and could be regarded as showing a minimum rejection either of pups of seven to ten days or at the age of the mother's litter. Nineteen to twenty-six day mothers, however, did not always accept test pups of the same age, and both the histograms concerned show a main dip in

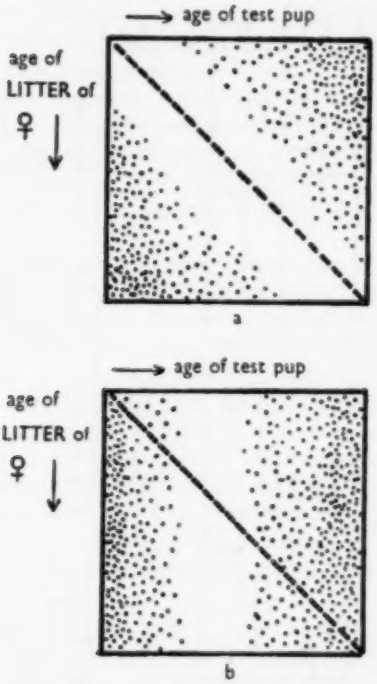

Fig. 2.—Two hypothetical interpretations of the distribution of results in the diagram Figure 1. Diagonals indicate reaction to own litter; stippled areas are those in which rejection of test pups may occur. Explanation in text.

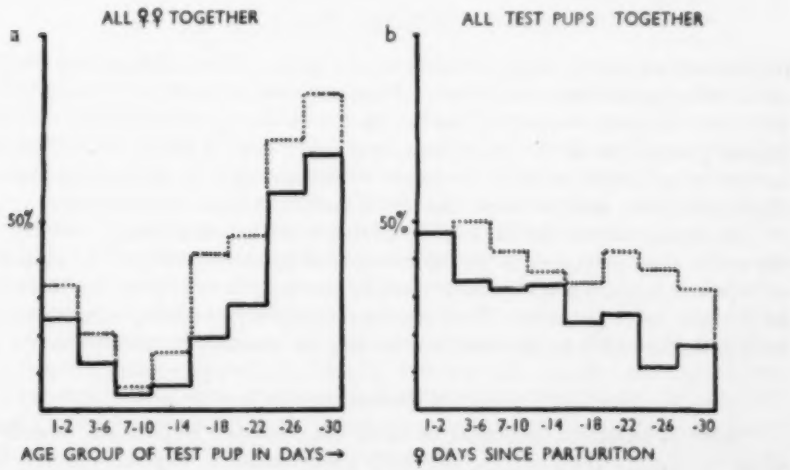

Fig. 3.—Responses of lactating females to strange pups. Solid line shows rejections, dotted line shows ambivalent responses, expressed as a percentage of the total tests at each age group. (a) is the sum of the histograms in Figure 4, and shows how females reacted to the different age groups of test pups. (b) shows the reactions of the different groups of mothers.

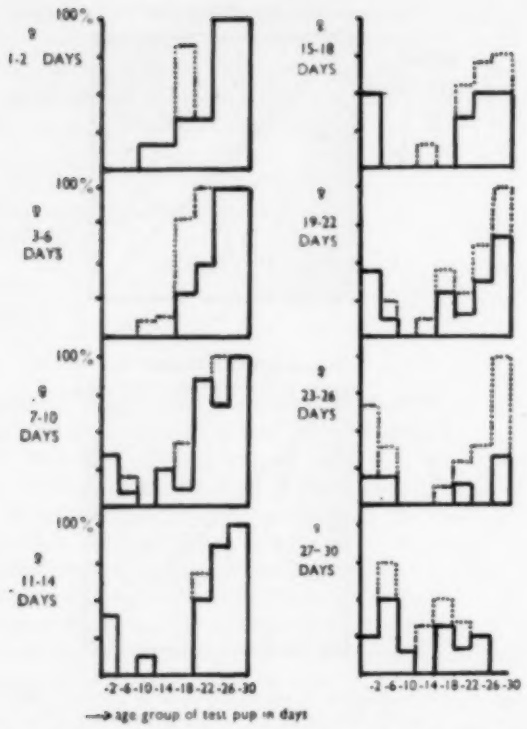

Fig. 4.—Responses of the mothers grouped according to the time since birth of their litters. Rejection shown as solid line, ambivalent responses as dotted lines, expressed as percentages of total tests with each age group of pups.

rejections for pups of seven to ten days with perhaps a subsidiary one for pups of the same age as their own litter. These mothers are very interesting because they have largely stopped retrieving their own pups, and yet they retrieve a higher proportion of test pups than any other groups (Fig. 3b). Thus they cannot be governed in their reactions to strange pups by their resemblance to their own litter, and therefore the first hypothesis is also inadequate.

The trend shown in Fig. 3b is perhaps rather surprising. Adding half the ambivalent responses to the rejections to simplify the picture, the proportion of rejected pups is seen to drop steadily during the course of lactation from 42 per cent to 24 per cent. This may perhaps be explained by a learning effect such as habituation to the family situation, or practice in retrieving.

Conclusions

There is sufficient evidence to show that neither hypothesis is sufficient alone to explain the findings, and both are required to explain different facts. The behaviour of the lactating hamster towards strange pups is shown to be influenced by (i) factors dependant on the time since the birth of her litter,

(ii) the relation between this time and the age of the test pup, and (iii) stimuli from the test pup which elicit maternal responses from any lactating female, and are optimal at seven to ten days.

It is generally assumed (Wiesner & Sheard 1933 ; Beach & Jaynes 1956) at least for the albino rat, that the younger the pup the more strongly it will elicit maternal responses, and similarly the neoparturient female is usually accepted to be " more maternal " than those which have been suckling for some time. Neither of these assumptions are born out by the results of this test series.

One group of factors influencing the behaviour, those dependent on time since birth of own litter, were selected for further analysis. These factors could be influencing the mother's behaviour directly or indirectly : the former would include changes in physiological balances, including hormone levels, which follow the birth of a litter, associated with the onset of lactation and its cessation after about three weeks. The latter includes changes in the stimuli provided by her own pups, which form an important part of the lactating females' environment, as they grow older. The litter could effect the female both by sensory cues and by feedback effects of its suckling activities on the milk secreting system. The influence of the pups and that of the female's own physiological processes, which normally change together from birth to weaning, can be separated experimentally by fostering a litter other than her own on to the lactating female.

TIMED RETRIEVING TESTS WITH " OWN " PUPS

The trends shown by females responding to strange pups described in the preceding section were not sufficiently sharply defined to be used for comparison with foster families. In search of a new parameter the behaviour of mothers retrieving their own pups was studied in more detail, and the components timed.

Control mothers with their own litters

Twenty-nine families were tested on alternate days until the mother no longer retrieved in the test situation, a stage usually reached about twenty-one days after birth although mothers were seen retrieving spontaneously for several days after this. Tests were begun with most females during the first three days after birth. Three families were not disturbed until day eleven or twelve, to show any effects of experience in the test situation : no such effects were observed, the results for these animals falling well within the range typical of the last half of the series started soon after birth.

Results : Timing was started when the female showed, by ear movements for example, that she was alert to the presence of the pup, and the time taken from this moment to picking up the pup was called *Reaction Time*. It included any preliminary investigation of the pup, but this was usually short or absent. The time required to cover the ground to the pup was very short, three to five seconds, and thus reaction time is primarily a measure of the animal's readiness to leave the rest of her litter and retrieve young. The figures obtained are shown in Fig. 5. There is a sharp increase in the occurrence of high readings at the beginning and end of lactation. Observation during testing made it clear that

these long delays before picking up had different origins at the beginning and end of the series. The neoparturient is brooding the rest of her litter and strong stimulation from outside is needed to make her change this activity : she may make preliminary movements to leave the nest and then " change her mind " and settle back again. The mother of a litter of weaning age on the other hand appears to delay picking up the pup because of lack of interest in young, and

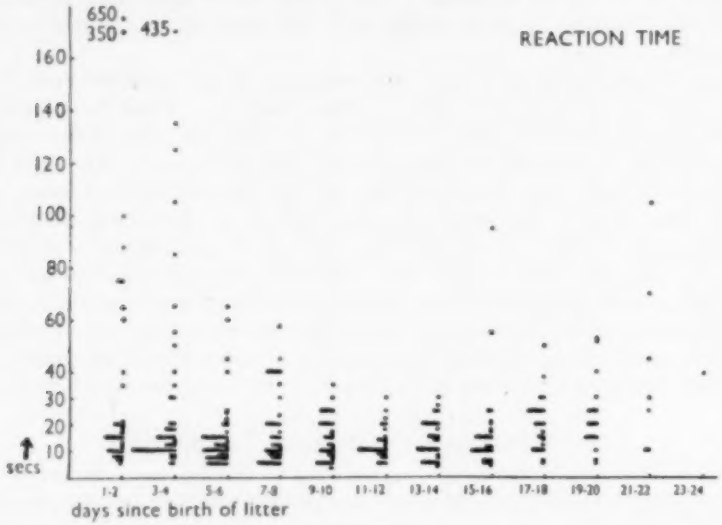

Fig. 5.—Retrieving tests with own pups : Times taken to react to the test pup.

she may sniff and leave it, or follow it for some time before making any attempt to pick it up. (The change to this type of response from the quick retrieving typical of days eight to fourteen and again to not retrieving at all, in the test situation, is very abrupt, and alternate day testing may miss the intermediate stage altogether. Individuals vary in the stage at which they change, so the massed results here give rather a different picture from the individual records.)

Retrieving time, measured from picking up the pup to putting it in the nest, remains remarkably constant at about ten to fifteen seconds, although the weight of the pup increases about tenfold during the series of tests. There is some slight evidence of a practice effect in this connection, a day to day increase in efficiency of handling young with practice being cancelled by a daily increase in weight and unwieldiness of the pups. If this is so, however, the practice effect must be short lived, because there was no sign of improvement with successive litters.

Licking time, measured from dropping the pup in the nest to turning to some other activity not directly concerned with the pup retrieved (usually either brooding the litter or going out of the nest) is shown in Fig. 6. It shows a steady and clearcut decrease during lactation, which can be seen in the records of each female as well as in the massed results shown. This trend was

sufficiently definite to be used as a basis for comparison between normal and foster mothers.

Mothers with foster litters

Twenty-three females were used.

6	maintained	2-6	day	litters
6	,,	6-10	,,	,,
6	,,	10-14	,,	,,
5	,,	14-18	,,	,,

Tests were again given on alternate days, i.e. two tests with each foster litter (see Materials and Methods), the first at least twenty-four hours, usually forty-eight, after the new litter had been given.

Figure 7 shows the licking times for foster mothers, plotted against the time since they gave birth to their own litters. There is no fall in licking time like that shown by the controls. Figure 8 shows the same data plotted with reference to the age of the litter with which the female was living, and hence also that of the test pup. Here the distribution is similar to that shown in the control group, with less licking by females living with older pups. Thus the behaviour of the mother in this context depends on stimuli from her pups rather than on factors independent of external stimuli.

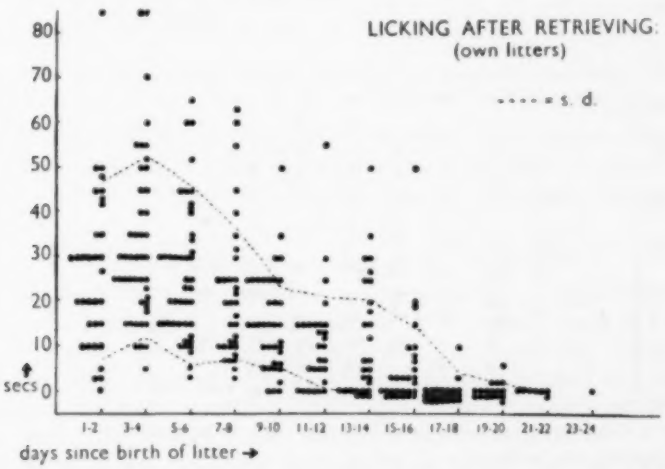

Fig. 6.—Retrieving tests with own pups: Times spent licking the test pup after having brought it to the nest. Dotted line encloses the standard deviations of the points.

Comparing control with experimental groups (Figs. 6 & 8) it will be noticed that the foster litters show rather more scatter in the eleven to eighteen day region, and the whole distribution is moved slightly to the right. To see if the poor condition of the foster litters was affecting the mother's behaviour, the licking time for the foster pups which had been weighed before testing (sixteen litters) was plotted with reference to the weight of the foster pups

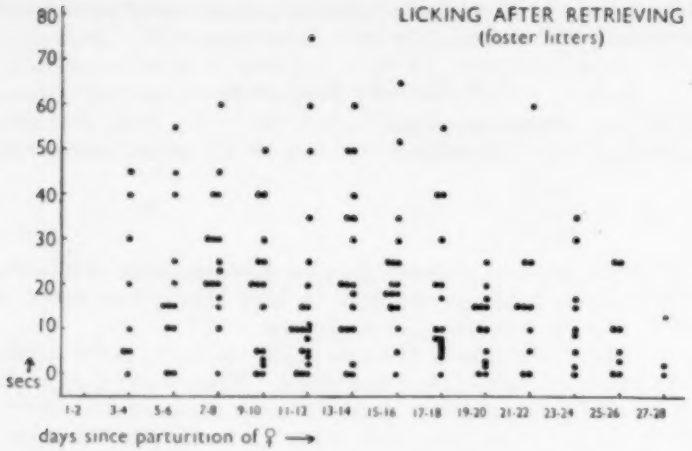

Fig. 7.—Mothers with foster litters. Times spent licking test pups after retrieving, plotted with reference to days since parturition of the mother.

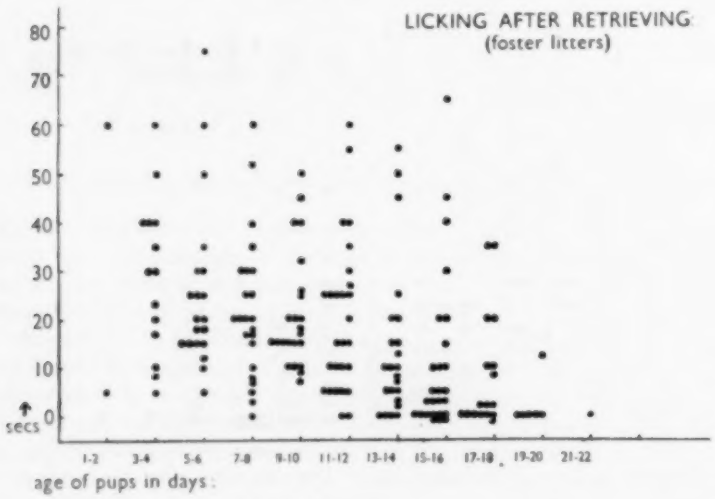

Fig. 8.—Mothers with foster litters. Times spent licking test pups after retrieving, plotted with reference to age of foster litter.

instead of their age. The normal pup with its own mother gains in weight at the rate of about a gramme a day from about two grammes at two days, so that over the time with which we are concerned its age in days is roughly the same as its weight in grammes. Foster pups which had had an unfavourable series of foster mothers were occasionally as much as six days behind their

age in weight. The result is shown in Fig. 9, and it can be seen that this graph corresponds much more closely to that of the control animals, suggesting that the smaller, undernourished pups were being licked longer than would be expected from their age. This does not necessarily mean, of course, that weight

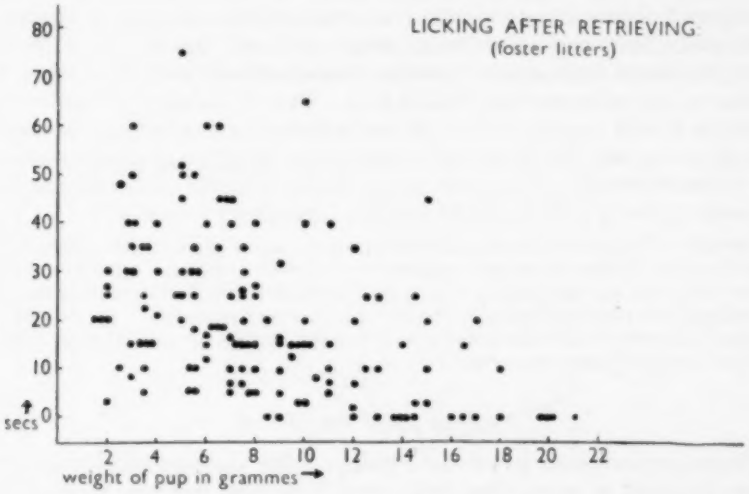

Fig. 9.—Mothers with foster litters. Time spent licking pups after retrieving, plotted with reference to the weight of the test pup. (Compare with figures 6 & 8.)

is the determining factor in the females' changing behaviour towards growing pups. Rather, weight is taken as an indicator of the mutiple effects of poor condition, including perhaps reduction of activity and possible retardation of development.

THE ACTIVITY OF LACTATING FEMALES

The results of the experiments on retrieving could be explained as being due to the foster mother being so influenced by the foster litters as to become equivalent, physiologically and behaviourally, to their own mother. For example the behavioural changes demonstrated could depend on changes in lactation in the female, and these in turn could depend entirely on the type of suckling (strength, frequency and duration) she received from her litter at different ages. There are some indications, however, that the females are not affected in this way, but that the time since her own parturition is a " meaningful " measure even to females whose litter is effectively prevented from growing up by the techniques of litter exchange described.

(i) *Duration of lactation*

The normal mother weans her litter at three or four weeks, the actual time varying with the individuals. Litters are occasionally seen suckling at thirty days. Milk supply of foster mothers with litters under fourteen days old is reflected in the appearance and weight gains of their pups. Of seventeen

animals which were given foster litters until they could no longer maintain them, seven litters began to look undernourished between twenty-four and twenty-eight days, eight between fifteen and eighteen days, and two at ten and thirteen days respectively.

Of those which stopped lactating under three weeks from parturition, nine of ten had litters under six days, whereas of the seven which stopped after three weeks, only three had litters under six days. According to Dieterlin (1959) pups begin to eat special maternal faeces at about five days, and from then on take an increasing amount of solid food. These facts suggest that there is a reduction in milk supply at about fifteen to sixteen days which can be survived by pups taking any solid food, and a cessation of milk flow at about three and a half weeks after birth. These changes are shown by mothers experiencing about the same quantity and quality of suckling throughout lactation.

Duration of lactation is probably species-typical in many mammals. Even dairy animals, which like those in these experiments experience a constant "suckling" type, do not usually lactate indefinitely, and the quantity of milk given varies with time since lactation in the normal way, although the absolute quatites are of course much greater than normal. On the other hand suckling is not without effect on lactation since a gland which is not emptied stops producing milk quite soon and begins to involute.

(ii) *Time spent out of nest*

During experiments it was noticed that foster mothers with young litters began to spend so much time away from their nest that the young became chilled. Data was therefore collected to see whether there was a gradual increase in time spent out of the nest during lactation, and if so whether it was effected by living with foster litters. Litters under weaning age spend practically all the time the mother is in the nest suckling, or at least gripping a teat. Thus the time the mother spends out of the nest is effectively the complement of the time available for suckling, and since the pups have no temperature control and rely on the female for a heat source as well, it is a measure of considerable biological significance.

Data from a continuous mechanical recorder showed that a record of time spent out of the nest during the first four hours of darkness (the period of maximum activity) adequately represented the level of activity in the twenty-four hours. All animals were watched during this time for several weeks, and every three minutes a note was made of whether each female was in or out of the nest. Control mothers with their own litters, foster mothers, and pregnant and unmated animals were observed. The measure used was the total number of observations at three minute intervals spent out of the nest during each four hour watch, expressed as a percentage of the total eighty readings per animal/day. (It was found in practice that the observations were sufficiently close to give in effect a continuous activity record.)

Results : There is a pattern recognizable in the records from individuals, although there is also a good deal of unexplained variation from day to day as well. Before mating there is a four day cycle correlated with the oestrous cycle, with peaks of almost continuous activity at oestrus, dropping to about 40 per cent in anoestrus. The day following mating little time is spent out

of the nest. During the rest of pregnancy time out of the nest is reduced somewhat below normal, and on the first day the litter is present there is a sudden further drop in activity, typically from 30 per cent to below 10 per cent. Then there is a gradual rise to a peak between three and four weeks followed by a slight fall off before the oestrous cycle reappears.

Data from all the control mothers were plotted together against number of days since birth (Fig. 10). Data from foster mothers were plotted against days since parturition of the mother and age of pups (Figs. 11 and 12). For

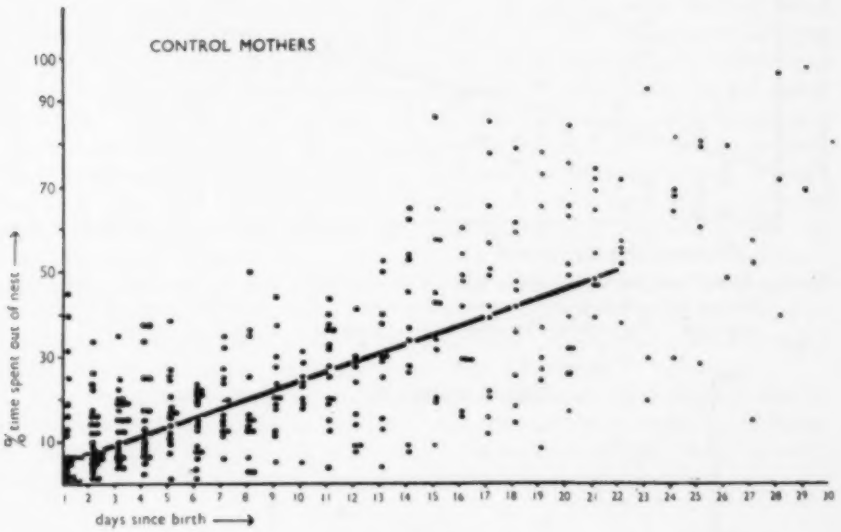

Fig. 10.—Time spent out of the nest in the first four hours of darkness by mothers with their own litters. (Line of regression equation drawn in.)

calculation data from mothers up to twenty days and foster pups up to eighteen days were used, since insufficient figures were available beyond these points.

In both control and foster mothers, time since birth is highly correlated with time spent out of the nest (controls $r=0{\cdot}66$, $P<{\cdot}001$; foster mothers $r=0{\cdot}5$, $P=<{\cdot}001$). Age of foster pups shows virtually no correlation with time spent by foster mother out of nest ($r=0{\cdot}1$, $P>0{\cdot}5$). If the equations expressing time spent out of nest in terms of time since parturition are plotted, the lines shown in Figs. 10 and 11 are obtained. The slopes and intercepts of these lines do not differ significantly (probability of the differences occurring by chance 0·6 and 0·5).

In Fig. 11, mothers with litters under nine days are shown as clear circles, those with litters over ten days as solid dots. It will be seen that the two groups are not arranged symmetrically about the best straight line given by the two groups combined.

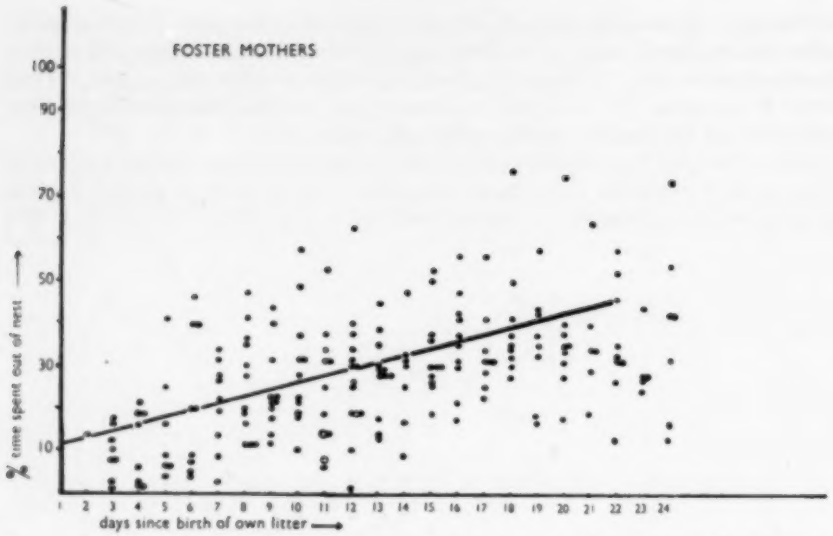
FOSTER MOTHERS
100
90
70
50
30
10
% time spent out of nest
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
days since birth of own litter

Fig. 11.—Time spent out of nest in the first four hours of darkness by mothers with foster litters. Plotted with reference to time since parturition of the female. Line of regression equation drawn in. Clear circles represent mothers with litters under nine days old.

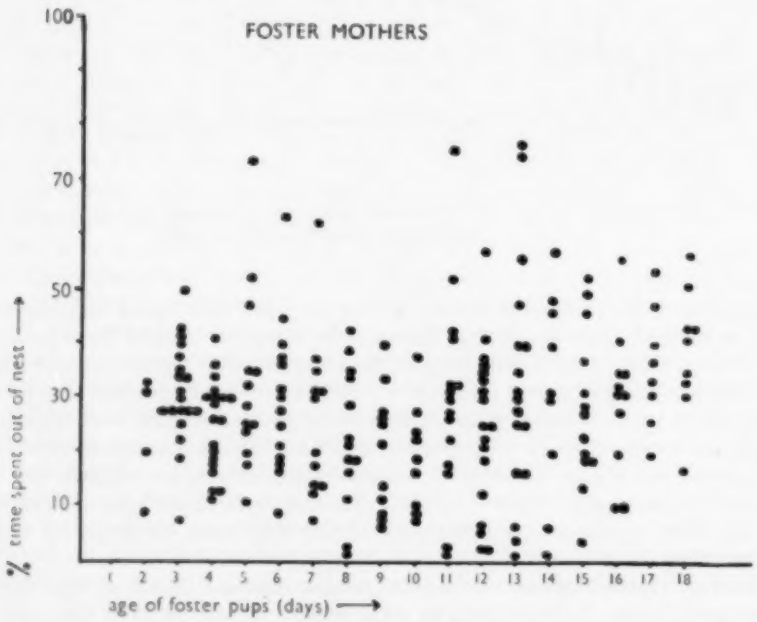

Fig. 12.—Time spent out of the nest by foster mother. Plotted with reference to age of foster litters.

The difference in the proportions above and below the line is in fact highly significant ($P<\cdot001$). Regression equations for the two groups give lines with the same intercept and slopes which are slightly, but not significantly different. That is mothers with older foster litters increase the time spent out of the nest slightly more quickly than do those with younger ones.

The most important determinant of the time a lactating female spends with her litter, then, is the number of days she has been lactating. Other factors also have their effect, however. Hunger and thirst, temperature, and other environmental factors play a part, and probably account for the day to day variation seen in individual records. The time spent out of the nest by all mothers gradually increases during lactation. The *rate* of increase is affected by individual " temperament ", some hamsters are always more active than others, and also, to an extent which is not statistically significant, by the age of her litter. From observation, it seems that the effect of the age of the pups is due to their starting to leave the nest themselves shortly before their eyes open. This would explain both the difference between foster mothers with younger and older pups and the slight step at fourteen to fifteen days which is shown when the mean values for two-day groups of control mothers are plotted. If the parameter " time spent out of nest " is taken to be the nearest available measure of time spent away from pups it will obviously become less accurate when the mother begins to find herself with two groups of pups, the litter in the nest and the wandering pup in the open cage : probably too much weight should not be placed, therefore, on these small differences.

Since time spent suckling and duration of lactation both depend almost entirely on the time which has elasped since parturition in normal and foster mothers, it cannot be maintained that a foster mother becomes behaviourally and physiologically equivalent to the mother of her foster litter.

DISCUSSION

Any of the behaviour patterns analysed in this study might have been used as a criterion of " maternalness "—the response to strange pups, the speed of response to presentation of the retrieving situation, the interest shown to a retrieved pup, or the time spent suckling. But if any of them had been used to quantify a " maternal drive ", the results would have been conflicting and misleading. Suckling time and licking after retrieving would have given a steady fall in drive intensity from birth to weaning ; reactions to strange pups would have given an equally steady *rise* ; whereas latency for retrieving would have given a humped curve.

The results also showed that these behaviour patterns are not governed by the same factors. Suckling time is dependent on factors within the mother, but the other patterns which are directed towards pups depend on external stimuli, received from the pups. These stimuli come both from the pup with which the mother is reacting at the moment and from the litter in the nest which is forming a background to the behaviour of a lactating female.

The concept of a maternal drive was introduced to explain the occurrence, only in the parent animal, of a group of mechanically unrelated activities whose combined result is care of young. The occurrence of maternal behaviour

in non-maternal animals has already been mentioned. Even in the lactating female, however, the maternal behaviour patterns are now seen to vary in ways unrelated to each other, which makes the concept of a unifying drive difficult to maintain. Again, though the drive is essentially an endogenous concept, most of the patterns analysed were found to change in relation to stimuli received from the environment and not to be dependent on some internal state of the mother.

As Hinde (1958) found of the "reproductive drive" when analysing nest building in canaries, the drive concept has not been helpful in explaining and discussing the observations described. It seems that for the moment at least, maternal behaviour can be most usefully analysed in relation to observable and measurable data, without recourse to theoretical concepts as intervening variables.

ACKNOWLEDGMENT

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THE PECTORAL ANATOMY OF *PANTODON BUCHHOLZI* PETERS (A FRESHWATER FLYING FISH) AND THE RELATED OSTEOGLOSSIDAE

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(With 9 figures in the text)

Pantodon buchholzi, a small west African osteoglossid, is thought to be a freshwater flying fish. Its expanded pectoral fins and its body-form would add credence to this supposition, whilst its pectoral musculature suggests the way in which flight could be effected.

Anatomical studies on the pectoral girdle and musculature show that both are remarkably developed and are probably unique amongst the teleosts. The girdle is characterized by the hypertrophy of its mesocoracoid and correlated hyperdevelopment of certain abductor and adductor muscles. Unlike the deep abductor muscles of other fishes, those of *Pantodon* originate on the *mesial* aspect of the girdle and pass to the exterior through an enlarged coracoid foramen. The large blocks of deep abductors fill the girdle and even surround part of the pericardium. The superficial abductors are also hypertrophied and even project posteriorly away from the body-line. The articulation of the pectoral fins is unusual since it does not allow the fins to be folded back against the body ; the only fin movement possible is in the vertical plane.

Apparently the pectoral musculature is highly adapted to spread and keep open the pectoral fins, at the same time imparting a powerful dorso-ventral motion to the fins. To this extent, *Pantodon* seems capable of true, flapping flight.

In both its pectoral osteology and myology, and in body-form, *Pantodon* differs markedly from other flying fishes. The latter, although belonging to numerous and phyletically distinct groups, all show convergent adaptations for flight.

The pectoral anatomy of the related Osteoglossidæ (*Heterotis niloticus* and *Osteoglossum bicirrhosum*) is described. That of *Heterotis* does not differ greatly from the generalized isospondylid type, but the anatomy of *Osteoglossum* is intermediate between the *Heterotis* condition and that of *Pantodon*. Many characteristics of the *Pantodon* girdle and myology are clearly foreshadowed in *Osteoglossum*.

The taxonomic status of *P. buchholzi* has long been uncertain, but the details of its pectoral anatomy and syncranial osteology clearly confirm its place in the Osteoglossidæ and suggest a relatively close relationship with *Osteoglossum* and *Scleropages*.

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INTRODUCTION

Pantodon buchholzi Peters 1876, the so-called butterfly-fish or African fresh-water flying fish is a monotypic genus occurring in the major rivers of western Africa (see Poll, 1957). Although generally recognized as related to the Osteoglossidæ, the exact status of *Pantodon* has remained uncertain since its discovery. Likewise, its reputed " flying " habits are still unproven although its ability as a leaper is well testified by numerous aquarists.

Apart from some details given in the original description (Peters, 1876) and Ridewood's (1905) careful study of the syncranium, no work has been done on the anatomy of this species. Originally we intended to re-examine the taxonomic position of *P. buchholzi* by basing our studies on the skull. In the course of this work, however, we found that the pectoral girdle and musculature were exceptional and had not been described. Furthermore, we could find very little published information on these structures in the Osteoglossidæ, the family presumed to be most closely related to *Pantodon*. A comparative study of the pectoral region therefore became imperative.

The results of this work are described below, together with a comparison of *Pantodon* with other flying fishes, particularly from the view point of their pectoral anatomy. Finally, the taxonomic position of *Pantodon* and its relationship to the other extant osteoglossids is reviewed.

COMPARATIVE MORPHOLOGY OF THE PECTORAL GIRDLE

As far as we know from published accounts (particularly those of Starks, 1930 and Grenholm, 1923) and from examining the osteological collections in the British Museum (Natural History), the pectoral girdle of *Pantodon* is unique. The most outstanding feature is the enlarged mesocoracoid and its spatial relations with other elements in the girdle.

Whereas in other isospondylid fishes the mesocoracoid is a small, narrow bone situated mesially to the cleithrum, in *Pantodon* the mesocoracoid is enlarged and flattened (reaching vertically almost to the tip of the cleithrum and having nearly the same width as the vertical arm of that bone) and occupies a lateral but somewhat mesially directed position adjacent to the cleithrum (Fig. 1). Despite its large area, the mesocoracoid is a thin bone, easily damaged during dissection. Its union with the cleithrum is by means of a slightly sinuous vertical suture. We cannot agree with Boulenger's (1909) description of this bone as " . . . slender, strongly curved, meeting its fellow on the median line ". The bone is only slightly curved and the left and right mesocoracoid arches are widely separated ; probably Boulenger was misled by the peculiar arrangement of the coracoid bones (see below).

The coracoid also departs from the usual condition in its marked posterior extension and the long foramen which occupies more than half the length of the bone. The postero-ventral limb of the coracoid is membranous and perforated by several small openings ; it lies mid-ventrally and then curves laterally and anteriorly. At the point of curvature, the left and right coracoids are in close apposition but are widely separated at their union with the mesocoracoid.

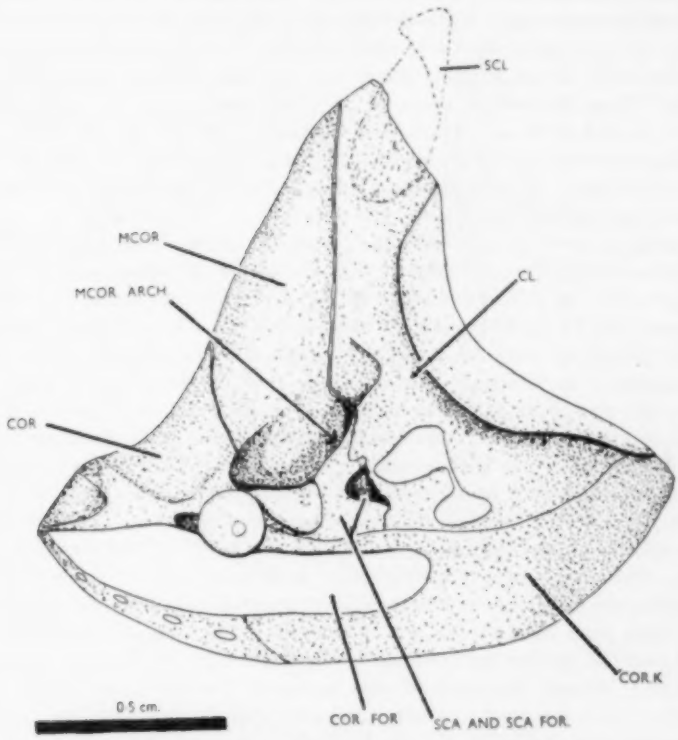

Fig. 1.—*Pantodon buchholzi* ; right half of the pectoral girdle, lateral view.
CL. cleithrum ; COR. coracoid ; COR. FOR. coracoid foramen ; COR.K. coracoid keel ; MCOR. mesocoracoid ; MCOR. ARCH passage through mesocoracoid arch ; SCA and SCA.FOR. scapula and its foramen ; SCL. supracleithrum.

Since the union is not clear in dry skeletons (where the coracoid and mesocoracoid appear continuous) this may have mislead Boulenger into thinking that the left and right mesocoracoids were united postero-medially (see above). The coracoid keel is but moderately well-developed and is relatively much smaller than the keel in, for example, *Chirocentrus* and *Ilisha* (Isospondyli) and considerably smaller than in the ostariophysine fresh-water " flying fishes ", *Gastropelecus* and *Carnegiella* (Characiformes, Gastropelecidæ).

In one specimen (used to prepare an alizarin transparency, see Fig. 1) there are two inter-connected foramina in the cleithrum, near its union with the

scapula ; no muscles, nerves or blood-vessels pass through these spaces which were not seen in two other specimens used for dissection.

The stout first pectoral ray articulates directly with the girdle by means of a long and broad, saddle-shaped surface developed on the scapula. The remaining seven rays are connected to the girdle in groups of three and four *via* two actinosts The anterior actinost has a concave head which articulates with a large, hemispherical boss on the coracoid ; the posterior actinost has a convex head that fits in the small, cup-shaped socket lying immediately behind the boss. Through this arrangement of articulatory surfaces the pectoral fin obtains considerable mobility in the vertical plane but virtually no horizontal movement is possible. Thus, the pectorals cannot be folded back along the body ; they can, however, be adducted and held close to the body with the long axis of the fin lying at an angle of about 25° from the vertical, often with the tips of the rays touching the water surface. Judging from photographs of *Pantodon* in aquaria, this is the usual fin position of the immobile fish.

A study of pectoral girdles in the osteoglossid genera *Arapaima*, *Heterotis*, *Osteoglossum* and *Scleropages*, shows that the girdle of *Osteoglossum* (and *Scleropages*) provides an annectant stage in the divergence of girdle form from the usual isospondylid type towards that of *Pantodon*. The girdles of both *Heterotis* and *Arapaima* may be considered typical isospondylid types, differing intergenerically in relatively minor details such as the shape of the coracoid keel and the size of the coracoid foramen (Fig. 2A). In both genera, the mesocoracoid is a small, narrow bone directed mesially and invisible when the girdle is viewed laterally. In *Arapaima* the left and right coracoids meet only at their anterior tips, but in *Heterotis* they are narrowly united.

Osteoglossum and *Scleropages* present a marked advance towards the *Pantodon* condition in the form of both the mesocoracoid and the coracoid (Fig. 2B and C). The mesocoracoid is lengthened and broadened, it is visible in lateral view and comes to occupy a more nearly antero-posterior and less mesially directed position than in *Heterotis* and *Arapaima*. The two coracoids are closely applied over the greater part of their mesial surfaces so that a true coracoid keel is formed. Indeed, the area of this keel is relatively greater than it is in *Pantodon*. The coracoid foramen is smaller than in *Pantodon* but larger than in *Arapaima* and *Heterotis*; also, it extends more posteriorly in *Osteoglossum*.

The articulatory surfaces for the pectoral fin in *Arapaima* and *Heterotis* consist of a simple, saddle-shaped surface and one large fossa immediately mesial to it ; both are borne on the scapula. There is a smaller and less well-defined fossa on the coracoid, barely separable from the scapula fossa. In these genera the pectoral fin can be held close against the body, with its long axis almost horizontal. In *Osteoglossum* and *Scleropages* there are, on the scapula, an enlarged saddle-shaped articulatory surface and one deep, well-defined fossa which partly undermines the posterior rim of the saddle. (This posterior horn is almost hemispherical in shape, thus fore-shadowing the hemispherical boss found in *Pantodon*. It seems likely that the boss in that species represents this hypertrophied posterior rim, especially since in *Osteoglossum* the rim is separated from the major articulatory surface by a narrow ridge and because it does not articulate with the first ray). The coracoid carries a

single fossa identical with that in the scapula and separated from it by a thin septum. There are three pectoral actinosts, the first being rectangular in shape and articulating with the posterior rim of the scapula saddle ; the other two are triangular, with hemispherical heads which fit into the scapula and coracoid

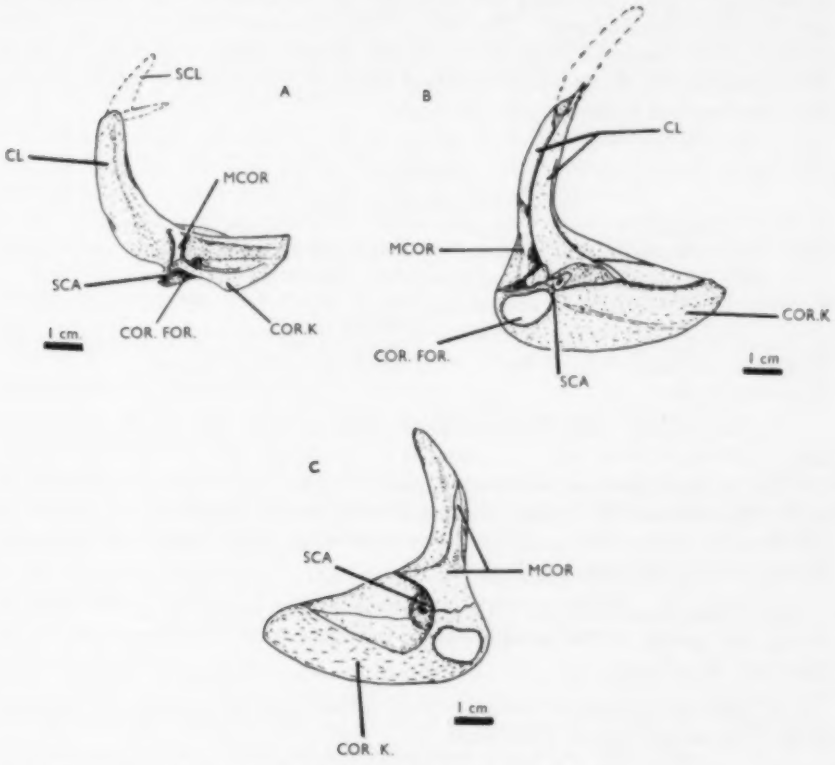

Fig. 2.—(A) *Heterotis niloticus* ; left half of pectoral girdle, medial view.
(B) *Osteoglossum bicirrhosum* ; right half of pectoral girdle, lateral view.
(C) The same, medial view ; the ' dashed " area is the zone of contact between the left and right halves. (For abbreviations, see Fig. 1).

fossæ. The insertion of the pectoral fin in *Osteoglossum* and *Scleropages* is roughly intermediate between that of *Pantodon* and *Heterotis* ; that is to say, although the fin can be folded back along the body it is held in the horizontal plane and not vertically against the body as in *Heterotis*.

MYOLOGY OF THE PECTORAL FINS

The atypical girdles of *Osteoglossum* and *Pantodon* are more readily understood when the musculature of the pectoral fins is taken into account. As might be expected, the pectoral musculature in the Osteoglossidæ shows various departures from the usual isospondylid condition, with that of *Heterotis* not differing markedly from the generalized type.

In *Osteoglossum*, and more especially in *Pantodon*, the place of origin of certain abductor and adductor muscles is unusual and even reversed with reference to the medial and lateral aspects of the girdle. As a basic reference in the comparative descriptions which follow, we have chosen *Salmo salar* as a generalized isospondylid type. The table below is based on Grenholm's (1923) descriptions and is somewhat simplified. Its chief purpose is to show where and from what aspects of the pectoral girdle the principal muscles arise. The insertions of these muscles remain relatively constant (even in *Pantodon* and the Osteoglossidæ) and are not considered in the table.

TABLE 1

The pectoral muscles of *Salmo salar*

Muscle	Origin
Mm. adductores (both superficial and deep)	Mesocoracoid ; *mesial* aspect of the coracoid, scapula and cleithrum.
M. arrector ventralis	*Lateral* aspect of the cleithrum, coracoid and scapula.
M. abductor superficialis	*Lateral* aspect of the cleithrum and coracoid.
M. abductor profundus	*Lateral* aspect of the coracoid.
M. arrector dorsalis	*Mesial* aspect of the cleithrum and coracoid.

The terminology used throughout the discussion is that of Grenholm (*op. cit.*).

The pectoral muscles of *Heterotis* differ slightly from those of *Salmo* and most other isospondylid fishes, but similar departure is seen in such fishes as *Chirocentrus* (Clupeoidei) and *Gnathonemus* (Mormyridæ). Briefly, the arrangement of the muscles is as follows :

M. adductor superficialis. Origin partly on the mesial aspect of the cleithrum and partly on the mesocoracoid ; it inserts on the dorsal aspect of rays 2–9 near their bases.

M. adductor profundus is closely associated with the *m. add. superficialis* both in its origin and its insertions.

M. arrector ventralis. A thin and somewhat tendinous muscle arising on the lateral face of the cleithrum, partly from the vertical arm and partly on the lateral expansion of the horizontal part ; the antero-ventral portion is covered by the upper part of the *M. abductor superficialis.* The *m. arr. ventralis* inserts on the anterior and ventral aspects of the first pectoral ray.

M. abductor superficialis. A large muscle (but relatively smaller than the *M. abd. superficialis* in *Osteoglossum* and *Pantodon*) originating on the lateral face of the cleithrum and coracoid ; it inserts on the ventral aspect of all rays except the first.

M. abductor profundus. A relatively small muscle (as compared with the *M. abd. superficialis* and with the *M. abd. profundus* in *Osteoglossum* and *Pantodon*) originating mainly on the mesial face of the coracoid with, perhaps, a few fibres from the mesial surface of the cleithrum. This muscle passes laterally through the coracoid foramen and inserts somewhat proximally to the

insertion of the superficial abductor. The disposition and origin of this muscle is not that of a typical isospondylid fish, but neither is it unique since a similar arrangement exists in *Chirocentrus* (Chirocentridæ) and *Gnathonemus* (Mormyridæ), as well as in certain members of other orders (e.g. *Alestes*, [Ostariophysi]).

M. arrector dorsalis. A relatively thick muscle which originates on the mesial face of the cleithrum and passes outwards through the mesocoracoid arch laterally to the proximal parts of the adductor muscles. Its insertion is on the dorsal face of the first ray.

Unfortunately, we could not dissect specimens of *Arapaima gigas* ; however, judging from the pectoral girdle it seems that there cannot be any great difference between the musculature of this species and *Heterotis*.

A more pronounced divergence from the generalized isospondylid type is seen in the pectoral muscles of *Osteoglossum* (and presumably also the closely related *Scleropages* which we did not dissect), see Figs. 3 and 4. The most outstanding difference, and one apparently as yet undiscovered in any other fish (except *Pantodon*), is the *lateral* origin of the adductor muscles and the predominantly *mesial* origin of the abductors. That is, a reversal of the usual condition in all teleosts.

Briefly, the muscle arrangement in *Osteoglossum bicirrhosum* is :

M. adductor superficialis has its origin mainly on the postero-lateral aspect of the mesocoracoid but a few bundles stem from the lateral aspect of the cleithrum ; it inserts on the upper surface of all pectoral rays slightly distal to the expanded basal portion of each ray.

M. adductor profundus. This muscle is not easily distinguished from the *M. add. superficialis* with which it shares a common origin. Its fibres insert onto the prominences at the proximal end of the fin rays.

M. arrector ventralis has its origin from the cleithrum and, at its anterior tip, from the coracoid keel. It inserts on the anterior and dorsal surfaces of the base of the first pectoral ray. The *M. arrector ventralis* is a relatively large muscle having a volume about half that of the two adductors.

M. abductor superficialis is a large, thick muscle, originating on the coracoid keel and occupying about three-quarters of the space between the lower edge of the keel and the ventral face of the lateral expansion of the cleithrum ; the remaining quarter is filled by the *M. arrector ventralis*. The *M. abductor superficialis* inserts onto the ventrally directed projection at the base of pectoral rays 2–6 but it extends more distally onto the seventh (*i.e.* last) ray, thus foreshadowing the posterior protuberance found in *Pantodon* (see below, p. 293).

M. abductor profundus (Figs. 3 and 4). This muscle is divided in two major portions, one of which we named the " twisted j " because its shape is that of the letter j with a single twist near the base of the vertical limb. The arrangement and origin of the *M. abd. profundus* in *O. bicirrhorsum* is one of the most outstanding features in the pectoral anatomy of the species and serves to set it apart from all other fishes yet described, except *Pantodon* (see p. 294). The " twisted j " originates partly on the mesial aspect of the cleithrum, partly

on the lateral face of that bone and partly on the postero-lateral face of the mesocoracoid ; it lies almost vertically along the posterior face of the girdle, closely applied to the mesocoracoid. At about the level of the mesocoracoid-coracoid suture it swings mesially and passes onto the inner face of the coracoid,

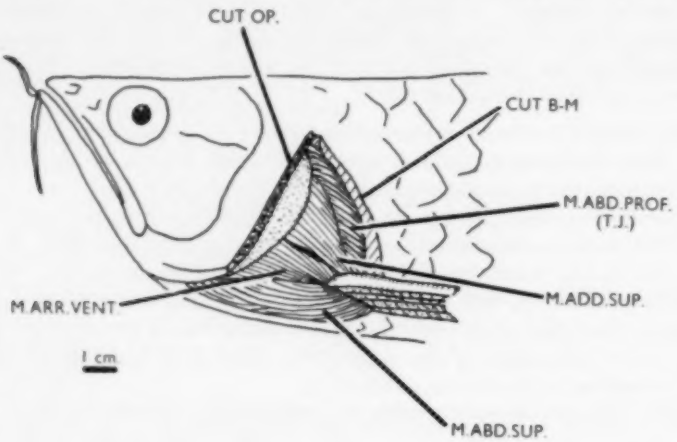

Fig. 3.—*Osteoglossum bicirrhosum* ; superficial pectoral musculature.
M.ABD.PROF. (T.J.) *abductor profundus* ("twisted j" portion); M.ABD. SUP. *abductor superficialis*; M.ADD.SUP. *adductor superficialis* ; M.ARR.VENT. *arrector ventralis* ; CUT B–M. cut edge of body muscles ; CUT OP. cut edge of operculum.

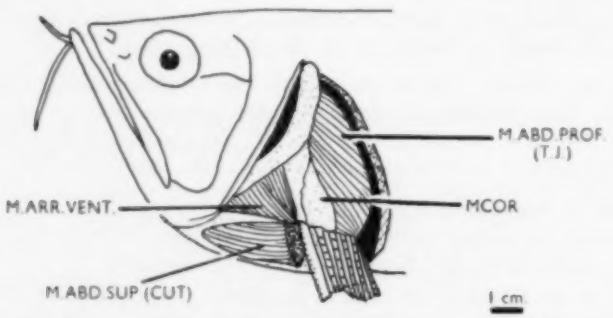

Fig. 4.—*Osteoglossum bicirrhosum* ; pectoral musculature after removal of the *adductor superficialis* and partial removal of the *abductor superficialis*.
MCOR. mesocoracoid ; other abbreviations as in Fig. 3.

immediately above the large coracoid foramen. It then turns laterally and passes to the exterior through the coracoid foramen. At this point, its fibres are not readily distinguished from those of the other part of the *M. abductor profundus*, a large and thick body of muscle originating on the mesial face of the cleithrum and mesocoracoid. This truly deep portion of the *M. abd. profundus* is a long muscle, extending nearly to the dorsal tip of the cleithrum

the left and right blocks almost fill the space between the two cleithra. Like the " twisted j " portion, the deep portion passes laterally through the coracoid foramen ; both parts of the *M. abd. profundus* have a somewhat tendinous insertion onto the ventral side of rays 2–7, at a point below and slightly proximal to the insertion of the *M. abd. superficialis*. We estimate that the volume of the *Mm. abductor profundus* and *superficialis* constitutes about 70 per cent of the entire pectoral musculature.

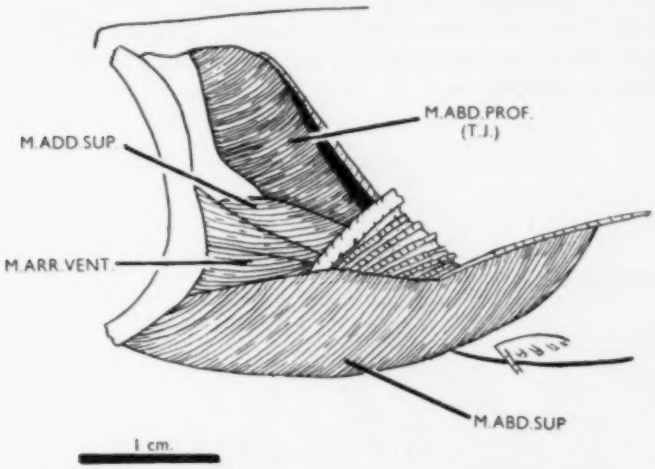

Fig. 5.—*Pantodon buchholzi* ; superficial pectoral muscles. (For abbreviations see Fig. 3).

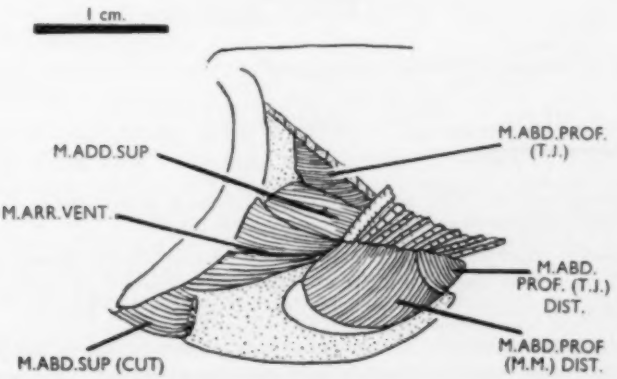

Fig. 6.—*Pantodon buchholzi* ; pectoral muscles after removal of the *abductor superficialis*, to show insertion of the *abductor profundus* muscles.
M.ABD.PROF. (M.M.) DIST. distal end of the main *M. abductor profundus* muscle ; M.ABD.PROF.(T.J.)DIST. distal end of the " twisted j " portion of the *M. abd. profundus*.

M. arrector dorsalis is a moderately well-developed muscle which originates on the mesial aspect of the cleithrum and, partly, on the coracoid ; its runs posteriorly and somewhat ventrally along the line of the coracocleithral suture and passes outwards through the mesocoracoid arch. It inserts on the upper surface of rays 2–5, immediately distal to the expanded proximal ends of these rays.

The pectoral musculature of *Pantodon buchholzi* is basically that of *Osteoglossum* (*cf* Figs. 3 and 4 with Figs. 5 and 6). What differences there are may be attributed to hypertrophy of the abductor muscles and the generally more compact nature of the entire pectoral musculature. Despite this latter character the pectoral region occupies a relatively greater volume of the body in *Pantodon* than it does in *Osteoglossum*.

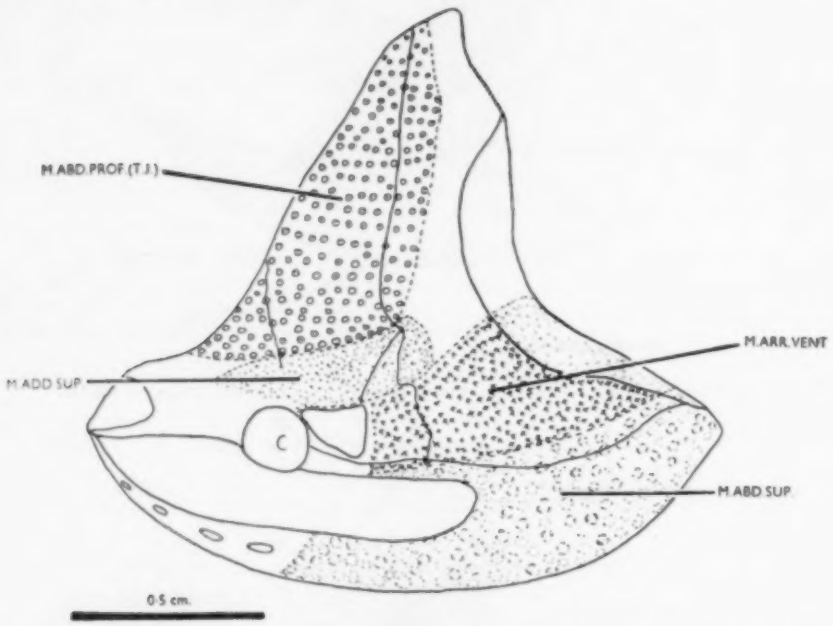

Fig. 7.—*Pantodon buchholzi* ; right half of the pectoral girdle in lateral view to show the origin of certain pectoral muscles. (Abbreviations as in Fig. 3).

M. adductor superficialis originates partly on the lateral aspect of the cleithrum and partly on the lateral face of the mesocoracoid ; it inserts onto the upper surface of pectoral rays 2–7, slightly distal to their bases.

M. adductor profundus. The origin of this muscle (which is largely overlain by the *m. add. superficialis*) is mainly from the mesocoracoid. Since, in relation to the *M. add. superficialis*, the *M. add. profundus* lies slightly more posteriorly, the part not covered by the former muscle is overlain by the " twisted j " segment of the *M. abductor profundus*. The insertion of the *M. adductor profundus* is slightly proximal to that of the superficial part.

M. arrector ventralis (Figs. 5, 6 and 7) is a moderately large but somewhat tendinous muscle apparently divided in two parts. It originates mainly from the cleithrum (lateral face) but a small portion has its origin on the coracoid. It inserts partly on the dorsal surface of the first pectoral ray and partly on its anterior and ventral surfaces ; a small slip also inserts on the ventral surface of the second ray.

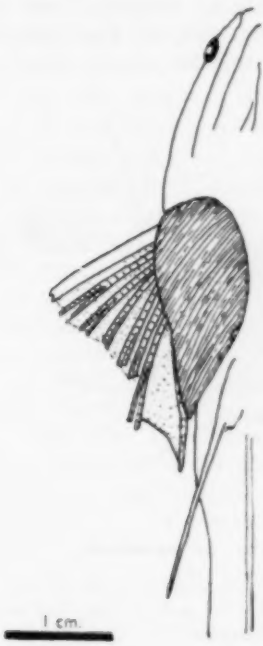

Fig. 8.—*Pantodon buchholzi* ; ventral view, after removal of the skin, showing the *M. abductor superficialis*.

M. abductor superficialis (Figs. 7 and 8). This muscle is one of the most noticeable features in the myology of *Pantodon*. Indeed, it is even visible without dissection because it forms a large, tear-shaped protuberance at the posterior end of the pectoral fin base ; the protuberance is adnate to and extends almost half-way along, the last pectoral ray*. Compared with the *M. abductor superficialis* of *Osteoglossum*, that of *Pantodon* has a much greater volume ; also, it extends further posteriorly although a faint indication of this extension can be detected is *Osteoglossum* (see p. 289). In *Osteoglossum*, however, only a

* Some drawings of *Pantodon* (e.g. those in Pellegrin [1923] and Bertin and Arambourg [1958]) are inaccurate in this, and other respects. In neither of the above mentioned drawings is the last pectoral ray shown as adnate to the posterior projection, which is omitted, although in Pellegrin's figure it is shown as connected with the pelvic fins. Furthermore in both drawings there are too many pectoral rays (9 or 10 instead of 8) and the shape of the caudal is incorrect. Probably the best figure available is that published with the original description (Peters, 1876).

small part of the last pectoral ray is adnate to the muscle. The *M. abd. superficialis* has its origin mainly from the coracoid keel (Figs. 1 and 7), but a small part arises on the antero-ventral region of the cleithrum ; it has short, tendinous insertions on the ventral face of branched rays 2–6 and a longer, more intimate union with the seventh (*i.e.* last) branched ray.

M. abductor profundus (Figs. 6 and 9). As in *Osteoglossum* this muscle consists of two major portions, a " twisted j " (see p. 289) and a large, nearly rectangular mesial block (see Fig. 9). The " twisted j " is proportionately larger than in *Osteoglossum* and lies almost immediately below the skin ; a

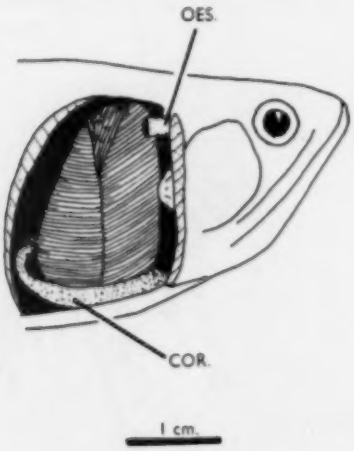

Fig. 9.—*Pantodon buchholzi* ; the main mass of the left *M. abductor profundus* as seen after the removal of the right half of the pectoral girdle and its associated muscles.
COR. coracoid ; OES. oesophagus.

few fibres of hypaxial body muscles run across it. So superficial is this part of the *M. abd. profundus* that, in an early dissection, we mistook it for part of the hypaxial musculature. Its origin is mainly from the lateral surface of the mesocoracoid and only partly from the lateral aspect of the cleithrum (Fig. 7). The position and ultimate passage of the muscle through the coracoid foramen are identical in *Pantodon* and *Osteoglossum*, except that in *Pantodon* it retains its identity after passing through the foramen ; it is easily distinguished from the main mass of the *M. abductor profundus* by the different direction of its fibres (see Fig. 6). The "twisted j" muscle inserts on the ventral face of the posterior pectoral rays.

The larger division of the *M. abductor profundus* originates from the inner face of the cleithrum and mesocoracoid (Fig. 9). It is by far the largest muscle mass in the pectoral system and actually fills the entire space between the vertical arms of the girdle. The muscle bulges mesially so that the left and right blocks are apposed in the mid-line. The oesophagus passes between the two masses which also surround the posterior part of the pericardium. As a result

of this extreme hypertrophy, the pectoral girdle and its musculature bulge into the anterior part of the peritoneal cavity.

We estimate that the abductor muscles (both deep and superficial) comprise at least 75 per cent by volume of the entire pectoral musculature.

M. arrector dorsalis. At its origin on the mesial face of the cleithrum, the *M. arrector dorsalis* is a broad and triangular muscle ; it narrows considerably as it passes through the scapular foramen and only a small portion is visible after its emergence. It inserts onto the dorsal face of the first pectoral ray.

SUMMARY AND DISCUSSION OF THE PECTORAL MUSCULATURE IN *PANTODON* AND THE OSTEOGLOSSIDAE

The pectoral muscles and girdles of *Heterotis* and *Osteoglossum* clearly show intermediate stages in the evolution of the *Pantodon* condition from that of the generalized isospondylid type. Two major trends are discernible in this series, first the rotation of the pectoral fin away from an oblique to a nearly horizontal insertion, and secondly, the hypertrophy of abductor muscles, particularly the *M. abductor profundus.*

The least modified condition is that of *Heterotis* (see p. 288). Here the *M. abductor profundus* shows some hypertrophy and has slipped through the coracoid foramen so that its origin is no longer lateral but mesial. Related to this shift is the fact that a larger area of origin is made available for the *M. abductor superficialis.* Naturally, the mesial origin of the *M. abductor profundus* has affected the architecture of the girdle but there is no marked change in the size and extent of the mesocoracoid. The pectoral fin in *Heterotis* is inserted obliquely and can be drawn back so as to lie flat against the fish's side.

The structural gap separating the girdles of *Osteoglossum* and *Heterotis* is considerably greater than that between the girdles of *Osteoglossum* and *Pantodon* (see p. 286 and Figs. 1 and 2). In all, the differences are attributable to the results of abductor hypertrophy and the change towards a horizontal insertion of the pectoral fin.

In *Osteoglossum*, the *M. abductor profundus* is greatly enlarged and also split in two major masses. The most obvious result of this hypertrophy is the heightened and antero-posteriorly expanded mesocoracoid (Figs. 2B and C). In turn, the enlarged mesocoracoid has brought the origin of the adductor muscles away from their typically mesial position into a lateral (albeit postero-lateral) one. The *M. abductor superficialis* is also markedly hypertrophied, especially in comparison with this muscle in *Heterotis* ; osteological consequences are manifest in the development of a large coracoid keel.

In *Pantodon* we see the ultimate development of the trend. Both the deep and superficial abductors are further enlarged with the result that the mesocoracoid has expanded until it is effectively a postero-medially directed continuation of the cleithrum (Fig. 1). The actual muscle arrangement in this species does not differ greatly from that of *Osteoglossum* except that the enlarged deep abductor and the expanded mesocoracoid have displaced the origin of the adductor muscles from a mesial to a lateral position on the girdle (*cf* Figs. 3 and 4 with Figs. 5 and 6).

We return to the phylectic implications of these observations in a later section (p. 299).

PROBABLE ACTION OF THE PECTORAL MUSCLES IN *PANTODON*

As we have not been able to get living or fresh specimens of *Pantodon* the supposed actions of the pectoral muscles have been derived entirely from observations made on preserved material.

The principle adaptive modifications of the pectoral musculature are, firstly, to spread and keep expanded the large pectoral fins, and secondly, to impart a powerful, almost vertical downward beat to the fins.

Muscles involved in spreading the fins are the *arrector ventralis*, the *arrector dorsalis* and, apparently, the *abductor superficialis*. Both arrector muscles are relatively powerful, the ventral one being split into two parts. Unlike the *M. arrector ventralis* in other fishes, that of *Pantodon* inserts on both the dorsal and ventral surfaces of the enlarged first pectoral ray, and on the ventral side of the second ray as well. The part played by the *M. abductor superficialis* is less clear. The last pectoral ray is adnate to a posterior prolongation of this muscle (see p. 293) and if the *M. abductor superficialis* and the arrectors contract simultaneously, the last ray will be pulled downwards and backwards. In this manner the trailing edge of the fin will be kept taut. Contraction of the *M. abductor superficialis* also assists in spreading the fin by moving the other pectoral rays forwards and somewhat ventrally.

The arrector muscles in *Pantodon* are peculiar in that there does not seem to be any set of muscles directly antagonistic to them. The only muscles which may fulfil this function are the posterior lobe of the *abductor superficialis* and the " twisted j " portion of the *abductor profundus*.

The action of the main, medially placed mass of the *M. abductor profundus* is more certain ; this muscle serves to impart a strong downward and slightly forward movement to nearly all the pectoral rays. The rays not moved by this muscle are the posterior two or three which are activated by the " twisted j ", whose action we could not determine.

As antagonists to the *Mm. abductores*, and especially to the *M. abductor profundus*, there are the comparatively small and short *Mm. adductores*. These pull the fin upwards and somewhat forwards. The *Mm. adductores*, together with the *Mm. arrectores* would seem to play an important part in maintaining the position of the pectoral fins when the fish is at rest. All published photographs of live *Pantodon* at rest indicate that the pectorals are kept expanded, with the upper surface held at an angle of *ca* 45° from the vertical and with a slight antero-posteriorly directed slope. According to eye-witness records, this fin position and immobility are maintained for long periods. Apparently no published account exists of the way in which the fish swims. It would be particularly interesting to know whether the pectoral fins take any major part in normal (as opposed to " take-off ") swimming movements.

The " flying " habits of *Pantodon* have been often and variously described, particularly in semi-popular publications (see especially Poll, 1953). We have made a careful check on the literature and as far as we can tell, no first-hand

account of flight has been published. A possible exception is J. S. de Brazza's designation of a *Pantodon* (which he collected and subsequently exhibited) as a "petit poisson volant" (Rivière, 1886). On the other hand, there are numerous reports by aquarists on the fishes' habit of leaping from tanks ; these accounts make it clear that *Pantodon* possess more than ordinary jumping powers and is apparently more inclined to jump than are most other aquarium fishes.

Pellegrin (1923) and Poll (1953) quite definitely describe *Pantodon* as a flying fish ; unfortunately neither author gives the source of his information. Poll (*op. cit.*) provides the more complete account of the flight but does not describe the manner in which the take-off is effected. Pellegrin (*op. cit.*), however, states "... s'elance hors du liquid en battant l'eau de ses nageoires ...". The two authors differ in their interpretation of the actual flight. In Poll's view, it is a gliding trajectory like that of the marine flying fishes, whilst Pellegrin's description calls to mind the semi-aerial surface taxi-ing (aided by the pectoral movements) ascribed to the south American characin freshwater flyers, *Gastropelecus* and *Carnegiella*. No one has yet claimed true flapping flight for *Pantodon* (as was recently claimed for *Carnegiella vesca* by Weitzman [1957]). But, of all the so-called flyingfishes, *Pantodon* would seem to have the greatest number of anatomical adaptions for wing-like movements of the pectoral fins.

Whatever the mode of flight in *Pantodon* both the body form and the pectoral musculature would be of great assistance in effecting a rapid take-off. The posterior concentration of the vertical fins should enable the fish to make short darts through the water at high speed, whilst the expanded and slightly inclined pectorals should act as hydrofoils by exerting a considerable lift force. The shape of the body, which closely resembles that of a flying-boat hull, would not impede any such movements ; indeed, its rounded and upswept anterior and knife-edge posterior ventral surfaces would tend to reinforce the lifting power of the pectorals.

We are ignorant of events, especially the action of the pectoral fins, once *Pantodon* is airborne. From Pellegrin's (1923) account it seems that *Pantodon* may use its pectoral fins as flapping wings and not merely as soaring planes. His statement " ... s'elance hors du liquid en battant l'eau de ses nageoires pectorales ... " is obscure in that one is unable to determine whether the fish shoots from the water as a result of beating the pectorals whilst it is still submerged or whether it keeps itself partly airborne by striking the pectorals against the surface (*i.e.* in the manner of *Gastropelecus* and its allies).

The pectoral musculature is clearly capable of imparting a flapping movement to the fin, the downward stroke being especially powerful. Also, the articulation of the fins allows them to be drawn through a very wide arc of about 95°. Considered from the hydrodynamic aspect, greater advantage would accrue from beating the fins against the surface than from a flapping movement carried out under water. If the fins were flapped under water the resulting forces would provide not only lift but a backwardly directed component as well. Thus any propulsive force provided by the normal swimming movements would have to be of sufficient strength to neutralize the backward component and still provide forward motion.

Without detailed field and aquarium studies further discussion can only become more speculative. We put forward these ideas in the hope that they may prompt some experimental work on this intriguing but neglected fish.

PANTODON COMPARED WITH OTHER FLYING FISHES

A comparison of *Pantodon* with other flying fishes serves to further emphasize its unique charcteristics.

As comparative subjects we have chosen both marine (Exocoetidæ [Synentognathi] and Dactylopteridæ [Scleroparei]) and freshwater forms (Gastropelecidæ and Cyprinidæ [Ostariophysi]). Data on myology are taken from Grenholm (*op. cit.*) and Rauther (1950), whilst gross morphology and osteology were studied from actual specimens.

Three outstanding superficial characters of *Pantodon* are its body shape (see above, p. 297), the virtually horizontal insertion of the pectoral fins and its inability to fold these fins back along the body. No other flying fish considered by us had a body-form like that of *Pantodon* ; the exocoetid body is subfusiform and almost quadratic in cross-setion, that of the dactylopterids nearly square, whilst in the gastropelicids and in *Pelecus* (Cyprinidæ) the body shows extreme lateral compression particularly along the entire ventral surface. The body of *Pantodon* is flattened dorsally with a rounded ventral cross-section anterior to the pelvic fins and knife-edged posteriorly. In fact, it combines the charcteristics of both the exocoetids and the gastropelicids.

None of the other flying fishes, except the Dactylopteridæ, have horizontally inserted pectoral fins and none is incapable of folding them back against the body.

Comparing pectoral fin shape and area we find that the " wing " of *Pantodon* is intermediate between that of the exocoetids and the gastropelicids. Treated as aerofoils the *Pantodon* pectorals have a low aspect ratio whereas *Gastropelecus* and *Carnegiella* have high aspect ratio fins.

There is considerable variation in the position, size and shape of the pelvic fins in these fishes. The filamentous type occurring in *Pantodon* is not found in any of the others, and, excepting the Dactylopteridæ, neither are the pelvics inserted immediately below the pectorals.

The caudal fin is deeply forked in the exocoetids, gastropelicids and *Pelecus* (Cyprinidæ), and somewhat emarginate in *Dactylopterus*. In *Pantodon*, however, it is rounded with the central rays produced beyond the margin.

In its deeper anatomy too, *Pantodon* stands apart from all other flying fishes and apparently from most other fishes as well (*Osteoglossum* excepted). Considering first the pectoral girdle we find that the Exocoetidæ, *Pelecus* and the Gastropelicidæ can be grouped together despite certain ordinal and generic differences. In all these fishes the coracoid keel is disproportionately enlarged, increasing in size from the exocoetid condition through that of *Pelecus* to the gastropelicid type. There are of course correlated changes in the size and distribution of the abductor muscles ; both Rauther (1950) and Ridewood (1913) discuss these points in great detail. The pectoral girdle in *Dactylopterus* is quite unlike that of the fishes discussed above ; in particular there is no hypertrophy of the coracoid. As would be expected, it is not a typical scleropareid

girdle (especially with regard to the horizontally and medially displaced scapula and coracoid) but its departure from the ordinal facies is less marked than that of *Pantodon*. There is a slight coracoid keel in *Pantodon*, but in all other characters the girdle of this species differs widely from that of the other flying fishes. Although unique, the *Pantodon*-type is obviously derived from the *Osteoglossum*-type. The peculiarities of the *Pantodon* girdle are partly conditioned by the presence of a mesocoracoid arch in the archetypal girdle from which it was derived. The potentialities of this girdle type were, however, not developed in other flying fishes ; for example in the Gastropelicidæ and in *Pelecus* (Cyprinidæ) the mesocoracoid remains small and consequently the associated musculature retains the typical lay-out (see p. 288).

Differences in pectoral fin musculature amongst flying fishes are equally distinctive. Again, *Pantodon* is the most atypical both in relation to other flying fishes and to other members of its order. The mesial origin and vertical disposition of the *M. abductor profundus* in *Pantodon* are characteristics not found in the other flying fishes, where the abductor muscles, although hypertrophied in varying degrees, are always lateral in origin and obliquely disposed.

THE TAXONOMIC POSITION OF *PANTODON BUCHHOLZI*

In his original description, Peters (1876) placed *Pantodon* in the Osteoglossidæ, but recognized it as representing a distinct and monotypic subfamily, the *Pantodontes*. There has never been any acknowledged doubt about the close relationship of *Pantodon* to the osteoglossids, especially after Ridewood's classic study on the skulls of these fishes (Ridewood, 1905). However, the exact status of the monotypic taxon *Pantodon* has varied from subfamilial (Peters, *op. cit.*), to subordinal (Berg, 1940).

The two most recent classifications (Bertin & Arambourg*, 1958 and Berg, 1940) give *Pantodon* the status of, respectively, a family in the suborder Osteoglossoidei, and, a suborder, the Pantodontoidei related to the Osteoglossoidei. Norman's classification (Norman M.S.) is the same as that of Bertin and Arambourg. In our opinion, the arrangement proposed by Norman, and Bertin and Arambourg is the most satisfactory because it stresses the uniqueness of the suborder as defined on dental and neurocranial characters (which *Pantodon* shares with the osteoglossids), gives adequate and balanced emphasis to the relationship of *Pantodon* to the other osteoglossid genera, and finally, shows the relatively close relationship of the osteoglossid genera *inter se*. Berg's scheme has the great disadvantage of over-emphasising differences between *Pantodon* and other osteoglossids, as well as exaggerating the slight differences between the various genera of osteoglossids ; according to Berg, each of the three principal forms of extant osteoglossids (i.e. *Arapaima*, *Osteoglossum* together with *Scleropages*, and *Heterotis*) should be raised to familial rank.

We have compared the differences between the osteoglossid genera and find that to those already known must now be added those connected with the

* There is an error in the list of subordinal characters given by these authors who state that the endopterygoid and opisthotic are absent. The complex articulation between the endopterygoid and the parasphenoid is a trenchant subordinal character ; the opisthotic is present in all genera except *Pantodon*.

osteology of the pectoral girdle and the myology of the pectoral fins (see p. 284). But, even when this information is combined with the other intergeneric differences there are still fewer fundamental dissimilarities between the genera *Heterotis*, *Arapaima*, *Scleropages* and *Osteoglossum* than there are between *Pantodon* and any one of them. *Pantodon* may be separated on seven characters, namely : thoracic position of the ventral fins ; nasals not suturally united ; premaxillæ united ; no opisthotic, no subopercular, extreme hypertrophy of the mesocoracoid and, finally, the greatly expanded and horizontally inserted pectorals.

However, on the basis of skull architecture and the structure of the pectoral girdle, one cannot fail to be impressed by the resemblance of *Osteoglossum* and *Scleropages* to *Pantodon*. The most outstanding similarities are in the general form and arrangement of the skull (especially the long, steeply inclined jaws) and the basically similar arrangements of the pectoral muscles and girdle elements. Other common characters are the dorsal position of the supraoccipital and the presence of a single articular head on the hyomandibular. In appearance the three genera are very different, particularly with regard to the size and position of the unpaired fins and in body-form. Although the sum of these structural differences is great, we are inclined to speculate that *Pantodon*, *Osteoglossum* and *Scleropages* were derived from a common ancestral stem within the ancient Osteoglossoidei. Perhaps *Pantodon* should be looked upon as the African representative of this sub-group, with *Scleropages* and *Osteoglossum* as, respectively, the Asiatic *cum* Australasian and American derivatives.

SUMMARY

1. The peculiar pectoral girdle of *Pantodon buchholzi* is compared with the girdle in extant osteoglossid genera. The girdles show progressive departure from the general isospondylid type, with that of *Heterotis* nearest the latter and those of *Osteoglossum* and *Scleropages* representing a basic type from which the *Pantodon* type could have evolved.

2. There is a corresponding degree of differentiation shown by the pectoral musculature of these fishes. In *Pantodon* and *Osteglossum* the *M. abductor profundus* is strongly developed and situated within the girdle. In *Pantodon* there are also changes in the origin of the adductor muscles. *Heterotis* does not depart radically from the generalized isospondylid arrangement of the pectoral muscles.

3. The probable action of the pectoral muscles in *Pantodon* is discussed. Whatever its actual mode of flight, *P. buchholzi* does at least seem capable of moving its expanded pectoral fins in a wing-like manner.

4. *Pantodon buchholzi* is compared with other flying and so-called flying fishes, both freshwater and marine. Its isolated anatomical position is emphasized by these comparisons.

5. In the light of the new anatomical information, the taxonomic position of *Pantodon* is reviewed. Its close relationship to the Osteoglossidæ is confirmed.

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THE FOOD AND FEEDING HABITS OF SOME HEATH-DWELLING INVERTEBRATES

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The larger, ground-dwelling invertebrates were collected from a heather moor in Dunbartonshire. The commoner species included *Bradycellus ruficollis*, *Olophrum piceum*, *Othius angustus*, *O. punctulatus*, *Quedius boops*, Aleocharina and *Neobisium muscorum*. After isolation in captivity they were offered various living animals and/or plants as food and records were kept, from March to August 1955, of the species and quantity eaten. The smaller staphylinids favoured the collembola but also ate some mites whilst *O. punctulatus* fed on the larger invertebrates. *Neobisium* ate the larger active collembola and *Bradycellus* fed on *Calluna* and a few collembola.

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INTRODUCTION

Although *Calluna* heathland covers large areas of the British Isles the investigation of its invertebrate fauna has attracted comparatively little attention. The most thorough examination of a heathland fauna appears to have been that of Summerhayes, Cole & Williams (1924) and Richards (1926) on Oxshott Heath, Surrey. Pearsall (1950) gave a general account of the invertebrates inhabiting various moorland types in the British Isles and more recently, Delany (1956) compared the faunas of three pioneer heaths in south-west England. These studies have been primarily concerned with recording the species present in various types of heathland. An alternative approach has been to select a group of heath-dwelling animals and study their ecology in detail. Examples are the work of Diver & Diver (1933) on grasshoppers and Lack & Venables (1937) on birds. The present study falls strictly within neither category. It attempts to analyse the food and feeding habits of the more numerous invertebrates within a limited area of heathland of uniform vegetation pattern. In this case the dynamic relationships of an animal community are the first consideration. The work has only been selective insofar as animals of a particular size-group have been examined. No attempt

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has been made to list all the animals present. The first collections were made on 17th March and observations were continued until early July, except for one species where they extended into mid-August, 1955.

THE AREA STUDIED

Collections were made on Carman Muir, Dunbartonshire (Grid. ref: 367787) at a height of just over 500ft. (152m.) above sea level. The vegetation of the portion of the moor sampled consisted of *Calluna vulgaris* 12–18 ins. (30-45 cm.) high and *Hypnum cupressiforme* var. *ericetorum*. The latter formed an almost continuous cover to the floor. These two species completely dominated the vegetation with no other plants observed within the area.

A record was kept of the relative abundance of the larger invertebrates by taking three, monthly samples between March and May, 1955. The March and April samples included all the moss and surface litter within an area of 5 m. × 5 m. whilst the May sample was taken from various parts of the survey area. The volume of moss and litter collected was recorded in each case and was subsequently sorted by hand. The commoner invertebrates are listed in Table 1.

TABLE 1

Numbers of invertebrates collected from Carman Muir, Dunbartonshire, March–May, 1955.

	13–17 Mar.	19–24 Apr.	27 May	
Vol. (cu. m.)	0·31	0·29	0·10	(0·30)
*Aleocharina	29	44	12	(36)
Bradycellus ruficollis	54	68	72	(216)
Neobisium muscorum	31	14	3	(9)
Olophrum piceum	22	21	3	(9)
Othius angustus	6	27	11	(33)
O. punctulatus	–	1	–	(–)
Quedius boops	†	1	4	(12)
Tachyporus obtusus	†	2	1	(3)

† no records.

Stenus not recorded.

* includes *Aleochara* and *Homalota*.

The May data have been made comparable with those for March and April by multiplying them by 3. The figures are given in brackets in the end column.

No comparable estimates were made of the abundance of the smaller invertebrates which provided the food of the larger ones. Thos selected were usually comparatively large, all were common and some *e.g. Onychiurus, Camisia* and *Pergamasus*, were very abundant. The following is a list of animals used, either as food or consumer, in the observations on feeding habits :

COLLEMBOLA

Isotoma sensibilis Tull.
I. viridis Bourl.
Lepidocyrtus lanuginosus (Gmel.)
Neanura muscorum (Temp.)
Onychiurus cf. *uliginatus* Gis.
Tomocerus longicornis (Müll.)

HEMIPTERA

Ulopa reticulata (Fabr.)

COLEOPTERA

Alecochara sp.
Bembidion sp.
Bradycellus ruficollis (Steph.)
Lathrimaeum unicolor (Marsh.)
Olophrum piceum (Gyll.)
Othius angustus Steph.
O. punctulatus (Goez.)
Quedius boops (Grav.)
Stenus impressus Germ.
Tachyporus obtusus (L.)

DIPTERA

Unidentified larvae

PSEUDOSCORPIONIDEA

Neobisium muscorum (Leach)

ARANEIDA

Various linyphiids

OPILIONIDA

Nemastoma lugubre Müll.

ACARI

Balanotium sp.
Bdella sp.
Unidentified belbids
Camisia biurus (Koch)
Ceratoppia bipilis (Herm.)
Johnstoniana sp.
Nanhermannia sp.
Pergamasus crassipes (L.)
Veigaia cervus (Kram.)

The list is not a complete record of all the species present in the *Calluna-Hypnum* association although it probably includes all the larger ground-dwelling species that are numerically abundant.

Except *Bradycellus* which is common on "heaths and sandy places" (Fowler, 1887) and *Ulopa* which is a heath-dweller (Edwards, 1896), the beetles, the false scorpion and the harvestman are ubiquitous (Fowler, 1888 ; Bristowe, 1949 ; Todd, 1949 ; Evans & Browning, 1954). The following collembola have been recorded from a variety of habitats : *Isotoma* (Stach, 1947), *Neanura* (Stach, 1951), *Lepidocyrtus* (Agrell, 1941 ; Weis-Fogh, 1948 ; Macfadyen, 1952) and *Onychiurus* of the *armatus* group to which *uliginatus* belongs (Weis-Fogh, 1948 ; Van der Drift, 1950 ; Macfadyen, 1952 ; Stach, 1954). *Ceratoppia* and *Pergamasus* are not restricted to heathland (Weis-Fogh, 1948 ; Macfadyen, 1952). The larger herbivores are more characteristic of heathland than the smaller ones and it is possible that the distribution of the latter is more influenced by the microhabitat provided by the layer of moss than by the presence of *Calluna*. Furthermore, it appears from their wider distribution that the collembola feed on a greater range of food than *Bradycellus* and *Ulopa*.

METHODS

The animals were extracted from the moss and *Calluna* litter using modified Tullgren funnels and were caught alive by placing a beaker containing damp filter-paper at the base of the funnel instead of one containing preserving fluid as is more customary. Although a number of animals escaped from the beaker, the method provided an adequate source of material. To maintain constant supplies of fresh food, frequent replenishments were obtained from the field.

The animals were placed in specimen tubes of one inch (25 mm.) diameter and either two or three inches (5·1 or 7·6 cm.) tall. A layer of wet cotton wool,

approximately half an inch (13 mm.) thick, was placed on the base of the tube and on top of this a circular disc of white filter-paper of slightly greater diameter than the tube. This facilitated the turning up of the disc around its edge and its close application to the side of the tube. Animals were then unable to penetrate into the cotton wool. Small crevices within the cork were filled with filter-paper and the cork rested, but not pressed hard, on the tube. Very small openings were thus left between the cork and the tube which permitted the entry of air and prevented the deposition of water vapour on the side of the tube. The openings were not sufficiently large to permit the passage of mites and collembola. The tubes were placed, away from direct sunlight, in an outdoor insectary.

Animals of one species were placed in a tube and animal food was added at intervals of one to nine days except for a period in April of seventeen days. As far as possible a surfeit was provided and attempts made to vary it as much as practicable. When introducing live animals as food, care had to be taken to avoid placing together carnivorous and herbivorous species if the former were at all likely to feed on the latter.

OBSERVATIONS ON FOOD CONSUMED

Aleochara sp.

Two groups were under observation ; the first contained two individuals from 26th April to 30th June and the second contained three from 30th May to 12th June and two from 12th to 29th June. *Onychiurus* was kept in almost constant supply and the quantity consumed was high ; for most of the period, between 0·5 and 2·5 *Onychiurus* were eaten by each beetle/day. *Balanotium*, *Veigaia*, *Lepidocyrtus*, *Isotoma sensibilis*, *I. viridis* and *Neanura* were also eaten but not *Camisia* or *Pergamasus*. On 4th July a single *Aleochara* was placed on damp filter-paper in a watch glass and offered *Camisia*, *Johnstoniana*, a belbid mite, proto- and deuto-nymphs of *Pergamasus*, a nymph of *Veigaia*, *Bdella* sp. and *Ceratoppia bipilis*. All were refused. It was then offered an *Onychiurus* which it took and ate immediately. Although the information on *Veigaia* is conflicting it nevertheless appears probable that this small staphylinid feeds largely on collembola.

Bradycellus ruficollis

Between 28th March and 25th May a group which varied between two and five individuals was offered *Onychiurus*, *Tomocerus* and *I. viridis* ; the last two were consistently refused as was *Onychiurus* except between 26th April and 5th May when a very small number were taken.

On 29th May faecal pellets were examined microscopically from thirty-two recently caught *Bradycellus*. Their contents were not readily identifiable and were compared with the dead flowers and leaves of *Calluna* and *Hypnum* leaves and stems. They compared most favourably with the *Calluna* leaves. Twenty-five *Bradycellus* were then equally distributed in five tubes. Five 1 cm. lengths of fully leafed *Calluna* stems were placed in four tubes; nothing was added to the fifth. The food was re-examined on 20th June. In one tube some leaves had been eaten as well as the tips of others ; in another a small

amount had been removed from one of the sprigs and in the remaining two a number of leaves had been torn off and left on the filter-paper plate. Little had been eaten in these two tubes. The *Calluna* leaves were replaced by sixteen old, fallen flowers. Re-examination on 12th August showed that some of the fruits had been partly eaten although two had been left sufficiently intact to permit the production of young shoots. All animals unfed since 29th May were still alive. A *Bradycellus* was observed, when removed from an extracting funnel, feeding on a fruit of *Calluna* on 12th June.

Olophrum piceum

Three beetles were placed together on 26th March and a fourth added on 2nd May. All thrived well until mid-June. They died between 12th and 26th June. *Bradycellus*, *Stenus*, *I. viridis*, *Onychiurus*, *Tomocerus*, *Camisia* and *Pergamasus* were fed upon freely until 30th May. Thereafter, although large numbers of *Bradycellus* were offered few were taken. The food eaten during this latter period included small quantities of *Aleochara*, *Othius angustus*, a linyphiid spider and *Tomocerus*. The reluctance to feed may have been due to changing environmental conditions. At this time of year the temperature in the insectary was probably appreciably higher than in the moss and litter. *Bradycellus*, *Othius*, *Stenus*, the mites and some collembola were dead when offered to *Olophrum*. Between 28th March and 6th April the insects bored a hole through the filter-paper and burrowed into the cotton wool. The filter-paper plate was replaced and no further attempts were made to penetrate it.

Othius angustus

A single specimen was kept from the end of March until early July and a second added from 28th March to 26th April and from 30th May to 26th June. Large numbers of *Onychiurus* were offered and seldom were any left uneaten ; the number consumed varied between 0·3 and 8·0 *Onychiurus*/beetle/day. Only from 2nd to 7th June was this animal offered and left untouched. *Tomocerus*, *I. viridis*, *Pergamasus* and *Camisia* were offered irregularly and although all four species were eaten a larger proportion of animals was left than was the case with *Onychiurus*. In addition, very small numbers of *Johnstoniana*, *Neanura* and small fly larvæ were eaten whilst *Bradycellus*, *Nanhermannia* and a belbid mite were not taken.

Othius punctulatus

One of the largest invertebrates inhabiting the moor it will apparently feed on a variety of animals. A single specimen was observed from 6th May to 27th June. Only *Olophrum*, *Aleochara* and *Nemastoma* were consistently refused. The species eaten were *Tomocerus*, *Ulopa*, *Neobisium*, a linyphiid spider, *Bembidion*, *Bradycellus*, *Lathrimaeum*, *Othius angustus* and *Quedius*. *Bradycellus* was offered in greatest quantity and up to two a day were eaten. This appears to be the maximum capacity of *Othius* as from 18th May there was an excess of *Bradycellus* in the tube. The remaining species were offered in small

quantities at irregular intervals and none were eaten in apparent preference for any other. *O. punctulatus* is an untidy eater leaving quantities of exoskeletal remains about the tube.

Quedius boops

Three beetles were kept captive from 28th March to 2nd April, one from then until 31st May and four from 31st May to 26th June. From 8th April *Quedius* ate, except for two short breaks totalling eight days when none were offered, between 0·3 and 2·5 *Onychiurus* per day. The quantity consumed varied from day to day ; thus between 16th and 26th June, although no other species was eaten and *Onychiurus* was constantly in excess, 1·6 animals/day were consumed by each beetle on the first three days, 0·6 the next four, 0·5 the next two and 2·3 the following day. The diet, at other times, was supplemented by small numbers of *Tomocerus*, *I. viridis*, *Pergamasus* and *Camisia* although the latter two species were rejected more frequently than they were taken. *Bradycellus*, *Johnstoniana*, *Lepidocyrtus* and a belbid mite were not taken.

Stenus impressus

A small active beetle capable of ascending the side of the tube. On 8th April, four *Stenus* were offered six, small, active, unidentified collembola. These were readily eaten. A single collembolan would be followed by a *Stenus* which on coming within stiking distance would crouch with head down, shoot out its labium and grab the insect between the palps. From 9th April to 30th June *Onychiurus* was in constant supply ; not more than 0·2/*Stenus*/day were eaten and frequently none were taken. *Lepidocyrtus* and *I. viridis* were likewise hardly touched. Compared with *Aleochara*, *Stenus* ate little food and left large quantities. Some nutrient was obtained from the food eaten as two *Stenus* placed without food on 8th April were dead by 26th April. *Ceratoppia* and *Camisia* were not eaten. On 16th June, three active mites were placed before a solitary *Stenus* ; one was grasped by the beetle but was released immediately. Sight appears to play a major role in the feeding of this insect. Furthermore, as it is a capable climber it is suggested that it may frequent the stems of *Calluna* in search of food. Six *Stenus* were placed together on 28th March and two removed on 8th April. One of the four was dead by 26th April and the next died by 5th May. The last two died at the end of May.

Tachyporus obtusus

A solitary individual captive from 9th April to 26th May was constantly supplied with *Onychiurus*. It ate between 0·2 and 1·0/day. A very small number (0·1/day) of *Lepidocyrtus* was taken between 18th and 26th May. *Bradycellus* and *I. viridis* were consistently refused.

Neobisium muscorum

Onychiurus and *Bradycellus* were offered to the pseudoscorpion until 26th May. The latter was not eaten and the former only sparingly (between 0 and 0·1/pseudoscorpion/day). There was evidence of cannibalism during this

period. A small *Tomocerus* was introduced into the tube on 26th May. On walking close to one of the false scorpions the insect was suddenly seized by a pedipalp and brought across to the mouth with the aid of the second pedipalp. It was then held against the mouth by the cheliceræ and the pedipalps released their hold. At this stage a second pseudoscorpion joined the first and took the free end of the insect between its cheliceræ. Both then fed upon the insect. This method of feeding was again witnessed on 12th June and is similar to that reported by Gilbert (1951) who found *Neobisium* reluctant to feed in the laboratory. From 26th May to 12th June *Neobisium* ate all the *Tomocerus* offered ; this varied between 0·1 and 0·2 *Tomocerus*/pseudoscorpion/day. During the same period a small amount of *I. viridis* was eaten but rather more refused. The readiness with which *Neobisium* took *Tomocerus* and its reluctance to eat *Onychiurus* suggest the former to more likely be its natural food. The number of pseudoscorpions used in the observations varied between two and seven ; several additions and removals were made and three were cannibalised. The last two died between 12th and 16th June. One of them was seen eating a *Tomocerus* on 12th June.

DISCUSSION

The interpretation of the foregoing data is difficult. The elimination of foraging due to confinement, the availability of food in quantity and the high insectary temperatures are all conditions different to those the insects would experience in the field. The latter may have been sufficiently high during early summer to be lethal to some species, *e.g. Neobisium*, *Tachyporus*, *Olophrum* and *Stenus*.

The surveys suggest that of the larger invertebrates collected *Othius angustus*, *Aleochara*, *Bradycellus*, *Olophrum* and *Neobisium* were the most numerous. They are assumed to be of major importance in the trophic relationships of the habitat. There was no direct evidence of any of these carnivores feeding on *Bradycellus* although *Olophrum* ate dead individuals of this species as well as of *Aleochara* and *O. angustus*. *Aleochara* fed freely on *Onychiurus* and was reluctant to eat mites; *Neobisium* appeared to favour the larger collembola and both *O. angustus* and *Olophrum* ate a variety of mites and collembola. *O. punctulatus*, a large and infrequent animal, fed upon *Neobisium*, *Bradycellus* and *O. angustus* but not *Aleochara* or *Olophrum*. This beetle will apparently exercise a major control over the numbers of larger invertebrates. It is not a highly selective feeder. Amongst the smaller animals *Onychiurus* was apparently fed upon more readily than *Camisia* and *Pergamasus* which were both numerous.

Laboratory conditions gave each species little opportunity to exercise any adaptations it may possess. Thus, *Quedius* has large eyes and probably hunts by sight, *Tachyporus* is an agile runner and *Stenus* a capable climber. As the carnivores are of widespread distribution it is assumed that they could feed on a variety of animals and it may be adaptations of this type that are of importance in fitting each species to a particular niche. Furthermore, a predator restricted to a particular microhabitat may never encounter in the field some of the animals offered to it in the laboratory. Other important

factors are probably the relative size of predator to prey, and the protection the herbivorous species may afford themselves by agility, thick resistant cuticles, cryptic coloration and unpalatability.

The foregoing attempts to analyse the feeding habits of the commoner species. The role of the less frequent species requires further analysis as do the feeding habits of the larvæ of the species already considered.

ACKNOWLEDGMENTS

Dr G. O. Evans identified the mites and Dr D. H. Murphy the collembola ; for their generous assistance the author wishes to record his thanks. He is grateful to Mr R. A. Crowson, not only for the identification of the beetles, but also for the constant interest and enthusiasm he has shown towards the work. He is indebted to Professor C. M. Yonge, C.B.E., F.R.S., for the facilities provided in his department and to Major Patrick T. Telfer-Smollett of Bonhill, M.C., for permitting the survey to be undertaken on his land.

SUMMARY

1. Collections of the larger invertebrates were made between March and June, 1955, from a *Calluna-Hypnum* heath in Dunbartonshire. Staphylinid beetles, *Bradycellus ruficollis* (a carabid) and *Neobisium muscorum* (a pseudoscorpion) were the most abundant.

2. These arthropods were placed in specially adapted specimen tubes and offered natural food mainly in the form of living mites and collembola. The tubes were placed in an outdoor insectary.

3. *Aleochara* fed mainly on collembola. *Olophrum piceum* ate a wider range of food, including some staphylinids, although much of it was dead when offered. Large numbers of collembola and some mites were consumed by *Othius angustus* and *Quedius boops*. *Othius punctulatus* fed on the larger invertebrates, including *Bradycellus* and several staphylinids. The small active collembola were favoured by *Stenus impressus* and the larger ones by *Neobisium*. *Bradycellus* fed on *Calluna* and a few collembola.

4. The implications and possible extension of this work are discussed.

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NOTES AND ABSTRACTS

MEETINGS OF THE SOCIETY FOR SCIENTIFIC BUSINESS

10th May 1960

PROFESSOR J. E. SMITH, M.A., Sc.D., F.R.S.

Vice-President in the Chair

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE : APRIL 1960

By L. HARRISON MATTHEWS, M.A., Sc.D., F.R.S.

The registered additions to The Zoological Society's Menagerie in London during the month of April were 105 in number, including some domestic animals. The following are of special interest : A Rufous Fishing owl *Scotopelia ussheri* Sharpe, new to the collection, presented by Mr J. Menzies ; a Horned screamer *Palamedea cronuta* presented by Mr Tom Spence ; three very young Giant tortoises *Testudo gigantea* presented by H.M. Government of the Seychelles ; two Common marmosets *Hapale jacchus*, three Jungle cats *Felis chaus*, three Spotted Eagle owls *Bubo africanus africanus* and two cormorants *Phalacrocorax carbo carbo*, born in the Menagerie ; a Spectacled bear *Tremarctos ornatus* and two Inca terns *Larosterna inca* (Lesson), new to the collection, received in exchange ; a male Black ape *Cynopithecus niger*, a female Smoky Woolly monkey *Lagothrix cana* and a female Great Grey kangaroo *Macropus canguru*, purchased to make pairs with existing specimens, and two Senegal Violet plantain-eaters *Musophaga violacea*, purchased. During the same period there were 39 additions to the Menagerie at Whipsnade Park, apart from transfers from London. The following are of special interest : four Père David's deer *Elaphurus davidianus*, a guanaco *Lama guanicoe*, a White-tailed gnu *Connochaetes gnou* and a White-bearded gnu *Connochaetes taurinus albojubatus* were born, and four Whooper swans *Cygnus cygnus* were hatched in the Park ; seven Common peafowl (white variety) *Pavo cristatus* were received in exchange from Paignton Zoo and four pandas *Ailurus fulgens* were received in exchange from Calcutta Zoo ; two Dufresne's parrots *Amazona dufresniana* were deposited by Mr P. H. Maxwell.

The following communications were read and discussed :

PROFESSOR A. J. E. CAVE. Ecology and dental pathology of the wild chimpanzee [To be published in the *Proceedings*].

PROFESSOR R. D. PURCHON. "The Malayan seashore" [Film].

DR DESMOND J. MORRIS. The origins of courtship displays.

14th June 1960

N. D. Riley, Esq., C.B.E., in the Chair

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE : MAY 1960

By L. Harrison Matthews, M.A., Sc.D., F.R.S.

The registered additions to The Zoological Society's Menagerie in London during the month of May were 172 in number, including some domestic animals. The following are of special interest : A young male Mountain gorilla *Gorilla gorilla beringei* which had become separated from the main group was picked up and cared for by the staff of the Uganda Game Department and this animal, together with a female chimpanzee *Pan satyrus* was made available for inclusion in the Society's collection. This is the second example of the Mountain gorilla to be exhibited, the previous specimen having lived here from 1938 to 1941 ; a pair of springhaas *Pedetes capensis* from Kenya and seven Prairie marmots *Cynomys ludovicianus* were purchased. The springhaas has not been exhibited since 1939, although two lived for a short time in the Quarantine Station in 1952 ; three Tacazze sunbirds *Nectarinia tacazze*, a Golden-winged sunbird *Drepanorhynchus reichenowi*, a Buff-bellied sunbird *Cinnyris venustus* and a Uganda Green-headed sunbird *Cyanomitra verticalis viridisplendens* were purchased for exhibition in the newly-arranged Tropical House ; births included a Senegal bush baby *Galago senegalensis*, five Great Field rats *Arvicanthis abyssinicus*, a Big-horned sheep *Ovis canadensis* and a Saiga antelope *Saiga tatarica* ; two Great Eagle owls *Bubo bubo bubo* and a cormorant *Phalacrocorax carbo carbo* were hatched ; Messrs G. H. and J. R. Newmark presented a collection of reptiles and amphibians from North Africa including a Bibron's agama *Agama bibroni*, four Algerian skinks *Eumeces algeriensis* and three Eyed skinks *Chalcides ocellatus*, a collection of sea-horses *Hippocampus kuda* from South-east Asia and 118 land invertebrates from North Africa including thirteen Desert scorpions *Buthus occidentalis*, forty Desert beetles and a Mole cricket *Gryllotalpa* sp., and also two-Red-headed tits *Aegithaliscus concinnus rubricapillus*, new to the collection, and two Himalayan Yellow-backed sunbirds *Aethopyga siparaja seheriae* ; a Quaker parrakeet *Myiopsitta monachus cotorra*, new to the collection, was presented by Mrs E. Wall ; two Pacific Coast hylas *Hyla regilla* were presented by Viscount Chaplin ; a Red-footed gannet *Sula sula rubripes* was presented by Captain D. Scorgie who has contributed the following information concerning it. It was picked up five months ago, when a chick, on Cocos Island and hand-reared by an American resident. Although taught to fly and given complete freedom, it never learned to fish for itself and always came back to dry land to be fed ; two Sclater's motmots *Momotus momota microstephanis*, new to the collection, were received in exchange. During the same period there were 38 additions to the Menagerie at Whipsnade Park, including some

domestic animals. The following are of special interest : two Black-necked swans *Cygnus melancoriphus* hatched in the Park, three Indian adjutant storks *Leploptilus argala* and two Lilford's cranes *Megalornis grus lilfordi* received in exchange from Southport Zoo ; a Mongolian wild horse *Equus przewalski*, a Burchell's zebra *Equus burchelli boehmi*, a Thomson's gazelle *Gazella thomsoni*, a Swamp deer *Cervus duvauceli*, a wapiti *Cervus canadensis*, two tigers *Panthera tigris*, a guanaco *Lama guanicoe*, two puma *Felis concolor* and a Père David's deer *Elaphurus davidianus*, born in the Park.

The following communications were read and discussed :

Dr F. C. Fraser. Photographs of the dolphin *Lagenorhynchus cruciger*.

Dr Kathleen Rigg, Dr R. Finlayson, Dr C. Symons, Professor K. R. Hill and Mr R. N. T-W-Fiennes. Arterial lesions in captive animals [To be published in the *Proceedings*].

Dr A. E. Hawkins, Dr P. A. Jewell and Miss Gillian Tomlinson. The metabolism of some British shrews [To be published in the *Proceedings*].

Dr J. R. Napier. Studies of the hands of living primates [To be published in the *Proceedings*].

Professor M. Hildebrand. Slow motion studies of the running cheetah and horse [Illustrated by a film].

WORLD REGISTER OF PERE DAVID'S DEER 1958/1959

By E. H. Tong, F.L.A.S.

The number of Père David's deer in the world today totals 456 and they are distributed over five continents. Of this total 356 are in Great Britain, the remaining hundred being in Canada, America, South Africa, Australia, China and the continent of Europe.

It is of interest to note that when this Register was first compiled in 1955 only eighteen Parks and Zoos were exhibiting these rare deer ; now they form part of thirty-one different collections.

It will be seen that both the Woburn and Whipsnade herds are slightly reduced in numbers from the last report.

Some years ago the herd at Whipsnade Park was divided into two—fortunately in the light of subsequent events, for in the spring of 1959 the original stock became infected with " Malignant Catarrh " and several animals died. The remainder were necessarily destroyed to prevent the spread of the disease to other ruminants. The second herd and all other species of deer escaped infection and the number of Père David's deer at Whipsnade Park is now increasing.

In the case of the Woburn Park herd the number were reduced by the culling of old stags and some of the older females.

	Herd 1957	No. Born	Deaths	Transferred to	Transferred from	Herd 1959
Adelaide Zoo	—	—	—		1 Taronga Zoological Gardens	1
Antwerp, Royal Zoological Society of	3	—	—	1 Barcelona, Parque Zoologico		2
Barcelona, Parcque Zoologico	—	—	—		1 Antwerp, Royal Zoological Society of	1
Basel, Zoological Garden	5	4	2			7
Berlin (East) Zoological Garden	5	1	—	2 Ruhe, L. Hanover		4
Berlin (West) Zoological Garden	2	—	1			1
Calgary, Zoological Society	—	—	—		1 Riverdale Zoo, Toronto	1
Chester, North of England Zoological Society	—	—	—		1 Lord Tollemache 1 Wellingborough Zoo	2
Chicago Zoological Garden	12	—	—			12
Cleveland Zoological Park	3	2	—			5
Copenhagen Zoological Park	8	1	1	3 Munich Zoo		5
Edinburgh Zoological Park	5	1	—			6
Edmonton, Alberta Game Farm	—	—	—		1 Riverdale Zoo, Toronto	1
Johannesburgh Zoological Park	2	1	1			2
Lindemann, Mr R. New York	1	—	—			1
Melbourne Zoo	—	—	—		1 Taronga Zoological Gardens	1
Milan Dr. Paladini	2	2	—			4
Munich Zoo	—	—	—		3 Copenhagen Zoological Park 1 Hannover Ruhe, L.	4
New York Zoological Society	8	1	—	1 Highland Park Zoo, Pittsburg		8
Paris Zoological Park	2	—	—			2
Pekin Zoological Garden	5	1	1			5
Pittsburg, Highland Park Zoo	—	—	—		1 New York Zoological Society	1
Prague Zoological Garden	3	—	—			3

	Herd 1957	No. Born	Deaths	Transferred to	Transferred from	Herd 1959
Pretoria, National Zoological Gardens	3	1	1			3
Regent's Park	1	—	—		1 Whipsnade Park	2
Riverdale Zoo, Toronto	6	—	1	1 Edmonton, Alberta Game Farm		3
				1 Calgary Zoological Society		
Rotterdam Zoological Garden	2	1	—			3
Ruhe L., Hannover	—	—	1	1 Munich Zoo	2 Berlin (East) Zoological Garden	—
Taronga Zoological Gardens	14	1	—	1 Adelaide Zoo 1 Melbourne Zoo		13
Tollemache, Baron of, Suffolk	1	—	—	1 Chester Zoo		—
Washington, Nat. Zoological Park	2	—	1			1
Wellingborough Zoo				1 Chester Zoo		
Whipsnade Park	23	13	18	1 Regent's Park		17
Woburn Park	324	194	183			335
						456

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NOTICE

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SYMPOSIA OF THE ZOOLOGICAL SOCIETY OF LONDON

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Papers submitted for publication are understood to be original works and are to be offered to the Zoological Society of London alone, unless the contrary is stated. They should be addressed to the Scientific Director, The Zoological Society of London, Regent's Park, London, N.W.1, and should be prepared in accordance with the Society's instructions to authors, a copy of which may be obtained from the Librarian and Clerk of Publications on application. The copyright becomes the property of the Society when a paper is accepted.

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